ABSTRACT

Title of Dissertation/Thesis:	THE EFFECT OF SEA LEVEL RISE ON SEAGRASSES: IS SEDIMENT ADJACENT TO RETREATING MARSHES SUITABLE FOR SEAGRASS GROWTH?
	Elinor Caroline Wicks, Master of Science, 2005
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Salt marsh retreat resulting from sea level rise creates new subtidal substrate (old marsh peat) for seagrasses, which is usually unvegetated. The hypothesis that sediment characteristics of old marsh peat are limiting to *Zostera marina* was tested in Chincoteague Bay, Maryland and in controlled experiments. A unique aspect of the study site is an eroding dune within the marsh that supplies sand to the subtidal. The organic content and sulfide concentrations of old marsh peat were not limiting *Z. marina* growth and seagrasses were able to colonize the old marsh peat if a layer of sand covered it. The lack of *Z. marina* in old marsh peat may be due to a plant morphology that is highly susceptible to dislodgement. These findings suggest that seagrass distribution may be negatively affected by sea level rise as seagrasses may be unable to migrate shoreward due to unsuitable sediments adjacent to retreating marshes.

THE EFFECT OF SEA LEVEL RISE ON SEAGRASSES: IS SEDIMENT ADJACENT TO RETREATING MARSHES SUITABLE FOR SEAGRASS GROWTH?

By

Elinor Caroline Wicks

Thesis submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
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Advisory Committee:
Associate Professor Evamaria W. Koch, Chair
Professor William C. Dennison
Professor J. Court Stevenson

DEDICATION

I dedicate this work to my mother, Christine Madison, to whom I owe so many of my accomplishments. I would like to thank her for all her love and advice through the years. Her constant faith and support has helped me to become a devoted scientist and compassionate human being.

ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. Evamaria Koch, for her guidance and suggestions. I would like to thank my committee members Dr. Bill Dennison and Dr. Court Stevenson for their advice and help at all stages of my thesis. I appreciate all the assistance and advice I received from Bill Severn. I appreciate the funding that has been provided by Horn Point Laboratory and the National Oceanic and Atmospheric Administration. It's been a pleasure to work with all the people at Horn Point Lab. I am deeply grateful to my family and friends for their patience and understanding.

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Introduction

Local impacts of sea level rise: retreating marshes and the availability of new seagrass habitat

A variety of global environmental parameters, such as atmospheric carbon dioxide levels, surface temperatures and sea level, have begun to change as a result of human activities (IPCC 2001). Global surface temperatures increased by an average of 0.6˚ C through the 20th century and are expected to continue to increase between 1.4˚ and 5.8˚ C by 2100 (IPCC 2001). The mean global sea level is expected to increase worldwide by an average of 0.09 to 0.88 m from its 1990 levels by 2100 (IPCC 2001). Global sea level rises as a consequence of increased surface temperature via the melting of glaciers and the expansion of water due to heating. The term "relative sea level rise" combines global sea level rise and land subsidence, which results from compaction of sediments over geologic time and groundwater extraction by humans (Ward et al. 1998). Relative sea level rise on Maryland's Eastern Shore is above average (3 mm y^{-1}) due to the higher rate of land subsidence (up to 1 mm y^{-1}, Rule 1995).

Global climate change and sea level rise are likely to affect terrestrial, coastal and oceanic systems. The consequences of sea level rise will especially be felt in coastal areas (Edwards 1995, Scavia et al. 2002). The negative effects of sea level rise include saltwater intrusion that may cause a shift in floral and faunal distribution, enhanced effects of extreme meteorological events, and increased erosion of shorelines (Edwards 1995, Scavia et al. 2002). A change in sediment depositional patterns, resulting from rising water levels, may also cause retention of fluvial sediment in the estuary instead of allowing it to move to the open ocean floor (Bird 1995). Arguably, sea level rise may

contribute to land subsidence, thereby compounding the problems of shoreline erosion (Scavia et al. 2002).

In addition to meteorological and geological effects, floral and faunal communities will also be influenced by global climate change (Eisma 1995). The effects of climate change on submersed vegetation, such as seagrasses, are still largely unknown. Possible effects include shifts in distribution patterns as a result of increased temperatures (Short and Neckles 1999) and decreased photosynthetic efficiency as a result of increased ultraviolet radiation (Dawson and Dennison 1996). However, increased productivity may result from higher carbon dioxide levels (Edwards 1995, Beer and Koch 1996). As global sea level rises, coastal plant communities including seagrasses are expected to move landward and may be able to colonize newly submerged areas (Kentula and McIntre 1986, Ehler et al. 1996). However, it has been postulated that the maximum depth limit of seagrass distribution is also expected to shift landward, and therefore, the total area available for colonization will probably not change significantly (Duarte 2002). The above statements regarding seagrass response to sea level rise are theoretical because the effects of sea level rise on seagrass distribution have not been studied directly. For example, increased shoreline erosion via sea level rise may limit seagrass colonization (Stevenson et al. 2002), thereby complicating the responses of seagrasses to sea level rise.

The effects of sea level rise on coastal salt marshes have been studied unlike the effects of sea level rise on seagrass beds. Salt marshes can be sustained as long as accretion rates equal or exceed the combined effects of land subsidence and eustatic sea-level rise (Stevenson et al. 1985, Ward et al. 1998). When salt marshes do not accrete at a sustainable rate, shoreline erosion occurs and results in salt marsh loss (Kearney et al.

2002, Stevenson et al. 2002). Additionally, as humans try to alleviate the problems associated with sea-level rise via the construction of bulkheads, dikes and seawalls, salt marshes will be caught between rising water and these man-made coastal erosion structures. This causes the available area for salt marshes to be reduced, possibly affecting the global carbon cycle and the invertebrate and fish communities that rely on salt marshes for habitat (Wilson et al. 1990, Hook et al. 2001).

In Chesapeake Bay and Maryland's Coastal Bays, marshes are eroding at a record rate, due to a combination of land subsidence and eustatic sea level rise (Stevenson et al. 1985, Kearney and Stevenson 1991). Interpretation of Landsat Thematic Mapper imagery indicates that 70% of all marshes in Chesapeake Bay are slightly to severely degraded (Kearney et al. 2002). The low-lying areas of the Eastern Shore of Maryland are especially susceptible to marsh erosion and indeed, current shoreline erosion maps show extensive erosion along all of Maryland's Coastal Bays (Maryland Geological Survey Maps 2005). For example, Mill's Island (Figure 1), located in the southwest corner of Chincoteague Bay (38° 03' N, 75° 18' W), has experienced substantial marsh retreat (0.59 m y^{-1}) over the past century (Figure 2).

In healthy coastal zones, seagrass meadows are commonly found adjacent to mangroves in tropical climates and salt marshes in temperate areas (Mitsch and Gosselink 2000) and processes occurring within mangroves and salt marshes are known to affect adjacent seagrass beds (Valiela and Cole 2002). Nutrients and organic matter are transported between marshes and adjoining ecosystems by tidal inundation (Whiting et al. 1989). Marshes are capable of taking up nitrogen and phosphorus from the water before it enters shallow water ecosystems colonized by seagrasses, reducing the direct effects of

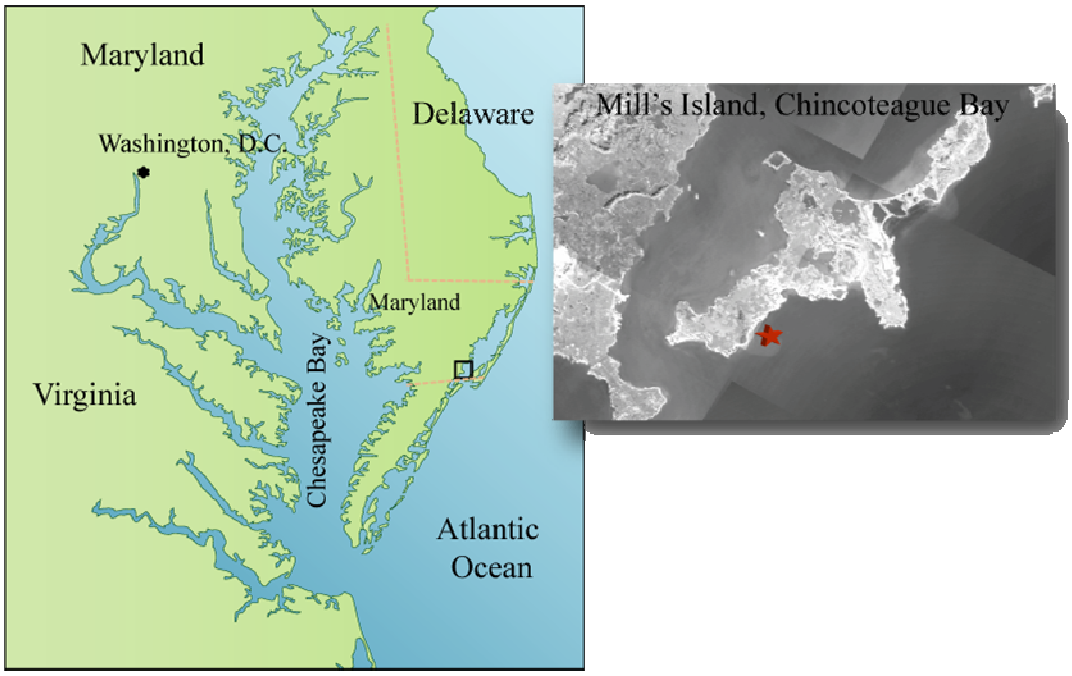


Figure 1: Location of study site ( ) at Mill's Island (38° 03' N, 75° 18' W) in Chincoteague Bay on the Eastern Shore of Maryland.

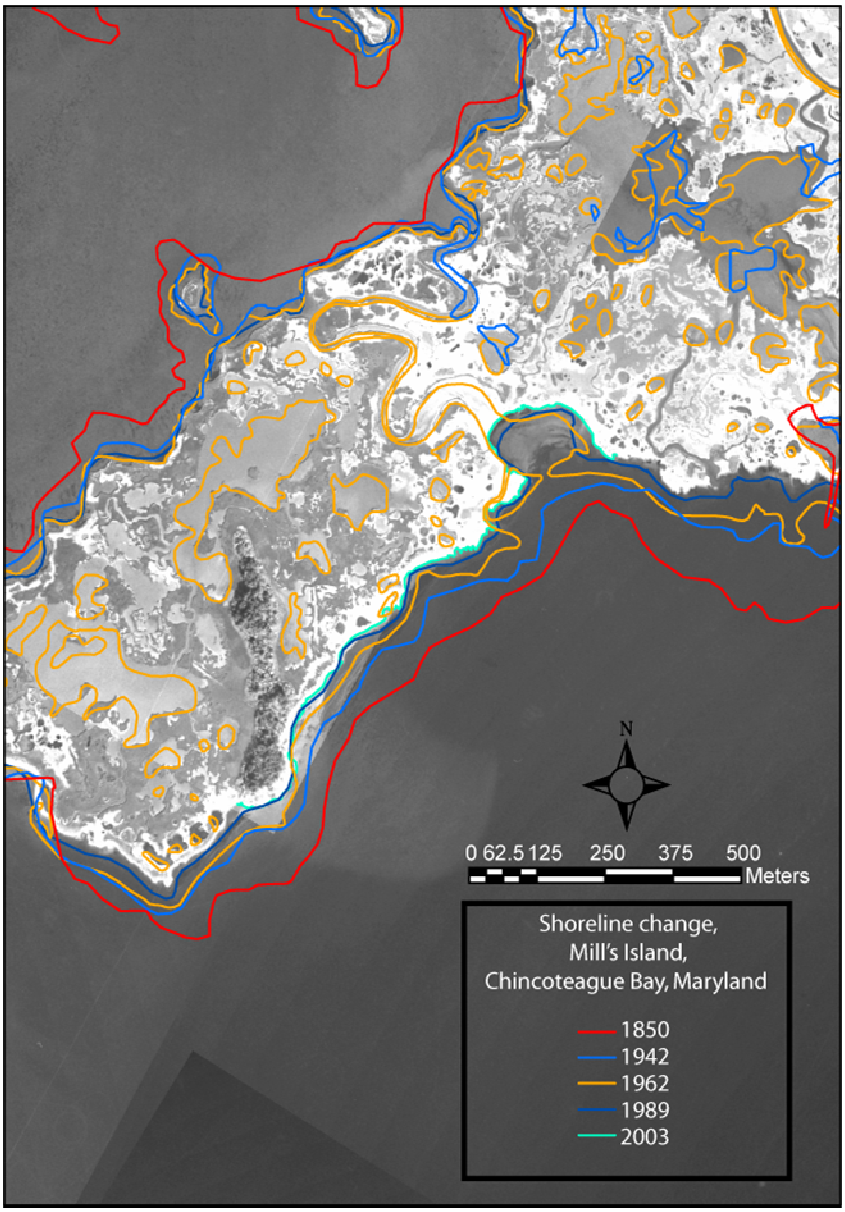


Figure 2: Historical shoreline change at Mill's Island, Chincoteague Bay, Maryland (1850 - 2003). Shoreline erosion was determined using Environmental Systems Research Institute, Incorporated's (ESRI's) ArcMap 9.0. First, historical shoreline vectors of Mill's Island were obtained from the Maryland Geological Survey (2005). Then, aerial photographs (Orth et al. 2002) from 2003 were digitized to determine the present shoreline. The shoreline was quantified by outlining the edge of the island to form a polyline shape. Finally, all years (1850, 1942, 1962, 1989 and 2003) were overlain to show the retreat of the shoreline

eutrophication on the seagrasses. Under some circumstances the average reduction in N loads to estuaries via fringing marsh denitrification and burial is sufficient to protect seagrasses from these high land-derived N loads (Valiela and Cole 2002). In tropical waters of Gazi Bay, Kenya, mangroves have been found to provide nutrients to the adjacent seagrass ecosystems as, during ebb flows, particulate and dissolved matter are transported from the mangrove forests to the seagrass beds (Kitheka 1997).

The link between adjacent systems is also seen in the associated fauna. Greater numbers of pinfish (*Lagodon rhomboides*) use intertidal marshes for predator protection and feeding habitat if they are adjacent to seagrass beds. Further, these pinfish are larger (higher weight) than in marshes adjacent to mud flats (Irlandi and Crawford 1997). This link between salt marshes and seagrasses is beneficial to commercially valuable species that use these habitats. From these studies, we can infer that adjacent ecosystems provide benefits not found in each system alone. However, the benefits of linked habitats may be affected by global climate change. For example, at Blackwater National Wildlife Refuge, in Dorchester County, Maryland, marshes have degraded extensively within the last century to form a large shallow embayment, surrounded by the remaining marsh (Stevenson et al. 1985, Stevenson et al. 2002). Seston levels reach values as high as 4 g l^{-1}, marsh erosion appears to have increased turbidity of adjacent waters and has led to seagrass loss (Pendleton and Stevenson 1983). Similarly, the suitability of shallow areas created by marsh retreat for seagrass habitat is unknown, although it has been speculated that the kind of substrate (mud versus sand) may affect the ability of seagrasses to colonize the area (Stevenson et al. 2002).

The motivation for this study was the unknown effects of sea level rise on seagrasses and the accelerated rate of shoreline retreat via relative sea level rise in Maryland. This thesis addresses the impact of marsh retreat on an adjacent seagrass bed at Mill's Island in Chincoteague Bay, Maryland. The shoreline at Mill's Island is a marsh barrier beach, which is characterized by a layer of sand over old marsh peat (Rosen 1980), and the adjacent subtidal is colonized by a seagrass bed. Based on a review of historical aerial photos, the loss of 59 m of marsh at Mill's Island over the last 100 years may have created a new subtidal area where seagrasses could potentially grow. Seagrass distribution is limited by light availability, as well as other physical and geological parameters (Koch 2001) and it is doubtful that seagrasses could grow in the entire area where marsh retreat has occurred due to depth limitations (Figure 3).

While light is the primary factor determining seagrass distribution, sediment organic content can affect the productivity and distribution of seagrasses (Cancemi et al. 2003, van Katwijk and Wijgergangs 2004). An organic matter content of 5% or more was found to inhibit growth of freshwater macrophytes (Barko and Smart 1983). A sediment organic content threshold for *Zostera marina* growth is currently unknown. Nutrient availability in the sediment can also affect seagrass growth and distribution (Short et al. 1990, Murray et al. 1992). Increased porewater ammonium and phosphate can increase seagrass growth; however, high porewater sulfide levels can be toxic to seagrasses (Murray et al. 1992, Duarte 1992, Kemp et al. 2004). Sediment organic matter and geochemistry are especially critical when evaluating seagrass habitat adjacent to retreating marshes.

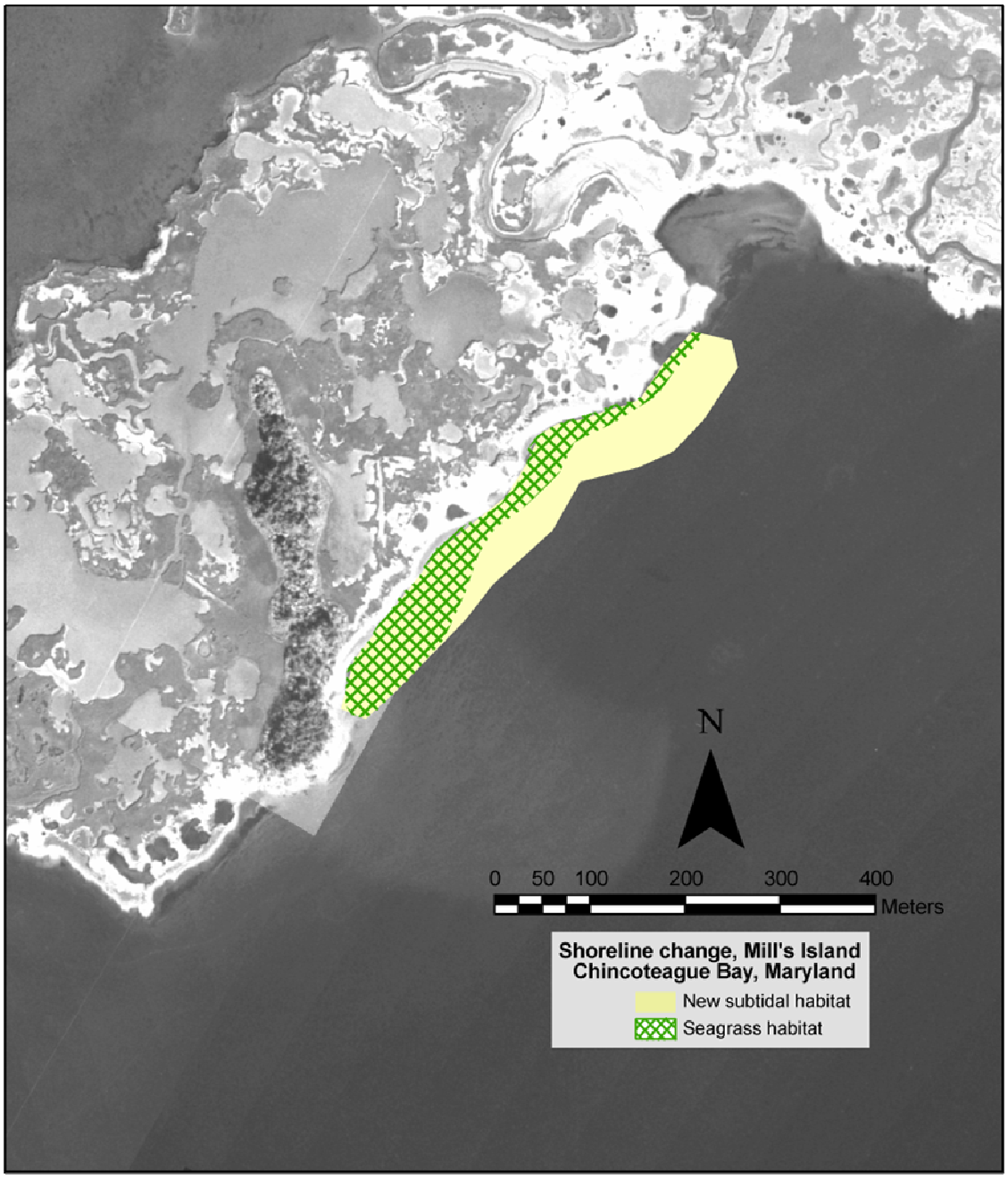


Figure 3: Potential seagrass habitat at Mill's Island, Chincoteague Bay. The yellow area represents the newly available seagrass habitat based on an erosion rate of 0.60 m y^{-1} for the last 100 years, i.e. marsh area lost in the last 100 years. The green hatched area represents current depths ≤ 1 m, which is considered the maximum depth for seagrass distribution at Mill's Island. Therefore, the hatched area represents the extent of the area where seagrasses can exist at present.

While erosional processes are exposing old marsh peat in the subtidal, there is also evidence that Pleistocene sand dunes within salt marshes are also being eroded (Rosen 1980, Mixon 1989). The sand from these eroding dunes is carried by currents and deposited over the subtidal old marsh peat. In areas where sand covers the old marsh peat, seagrasses appear to be able to grow immediately adjacent to the retreating marshes. Therefore, the objective of this study was to determine if the subtidal sediment found adjacent to retreating marshes is suitable for seagrass growth. Three hypotheses were tested.

Hypothesis 1: Organic content of sediments adjacent to retreating marshes (i.e. old marsh peat) is limiting to seagrass growth.

Hypothesis 2: High sulfide levels found in sediments adjacent to retreating marshes are limiting to seagrass growth.

Hypothesis 3: The type of substrate (sand versus old marsh peat) determines seagrass growth adjacent to retreating marshes.

These hypotheses were tested using a combination of *in situ* observations and controlled experiments. The methodology and findings for each hypothesis are addressed in the following chapters.

Chapter 1

Old marsh peat as seagrass habitat substrate: Does sediment organic content have an effect on seagrass growth?

INTRODUCTION

Seagrasses are marine angiosperms that colonize shallow coastal waters. They are an important component of coastal ecosystems, on a global and local scale. Growing in both the intertidal and subtidal zones, seagrasses stabilize sediments, attenuate waves, and create habitat for a variety of associated species (Dawes 1981, Stevenson 1988, Fonseca and Cahalan 1992, Hemminga and Duarte 2000). The distribution of seagrasses along coastlines is determined by light, temperature, salinity, waves, currents and sediment characteristics (Koch 2001).

The depth of seagrass distribution is limited by light availability. *Zostera marina* needs approximately 20% of the surface irradiance in order to survive (Dennison et al. 1993). In general, seagrasses can be found in a wide range of salinities, from about one-third to full strength seawater and can tolerate a wide range of currents and waves (Stevenson 1988). While gentle current velocity and mild wave action are essential for successful pollination (Ackerman 1986, Sullivan and Titus 1996) and photosynthesis (Fonseca and Kenworthy 1987, Koch 1994), storm events leading to erosion and resuspension of sediments can smother seagrasses (Short and Neckles 1999, Mills and Fonseca 2003). Although nitrate, phosphate, and ammonium in the water column and in the sediment porewater provide nutrients needed for seagrass growth (Hemminga and Duarte 2000), an overload of nutrients (eutrophication) stimulates epiphytic growth on

seagrass leaves and microalgal growth in the water column, negatively affecting seagrass growth by blocking light (Bulthuis and Woelkerling 1983, Lapointe et al. 1994).

While many studies have focused on light (Dennison 1987, Duarte 1991, Dennison et al. 1993, Livingston et al. 1998, Longstaff and Dennison 1999) and water quality (Stevenson et al. 1993, Moore et al. 1996, Meyercordt and Meyer-Reil 1999, Tomasko et al. 2001) as the primary parameters affecting seagrass distribution, other environmental factors are also important determinants of seagrass distribution and colonization but have received less attention (Koch 2001, Kemp et al. 2004). For example, in Danish coastal waters, seagrasses do not colonize all areas that meet the light requirements (<1 m to 8 m, Krause-Jensen et al. 2000, Krause-Jensen et al. 2003). Instead, seagrass patchiness and bare areas are observed at all depths despite light, wave exposure, and salinity requirements being met. When plotted against depth, the seagrasses percent cover exhibits a bell-shaped pattern. Extreme wind events (i.e. waves) may play a role in the lower percent cover of the seagrasses in shallow waters, while light is limiting in deeper waters (Krause-Jensen et al. 2003). Not only storm-induced waves can limit seagrass growth but also substrate type. In Biscayne Bay, Florida, *Thalassia testudinum* beds are found in circular depressions that are filled with mangrove peat overlaid by calcareous mud and shell fragments (Zieman 1972). The substrate of the bay is mainly limestone bedrock interspersed with Karst topographical features. Mangrove hammocks formed in these depressions. However, as sea level rose over the last millennium, the mangroves died and *Thalassia* now colonize these areas. Further studies like these are needed to address the effects of parameters other than light on seagrass distribution.

While seagrasses seem to be able to colonize a variety of sediment types (Table 1), in-depth studies of the sediment requirements for seagrasses are lacking and existing data is contradictory. For example, one study sampled a *Zostera marina* bed in which the sediment organic content was 9.93% dry weight (Holmer and Laursen 2002), which is considerably higher than the range generally accepted for this species (5%, Koch 2001). In freshwater environments, it has been stated that sediment organic content above 5% is limiting to freshwater macrophyte growth (Barko and Smart 1983).

The study of sediment organic content in seagrass habitats is especially important when marsh retreat via sea level rise is occurring. As marshes retreat, newly formed subtidal areas are available as seagrass habitat (Figure 1). The substrate of these newly formed areas is old marsh peat, which usually has high sediment organic content and therefore, may be limiting to seagrass growth. Understanding if sediment organic content of old marsh peat is limiting to seagrasses will allow the prediction of the future of seagrasses adjacent to retreating marsh shorelines. Sea level is expected to continue to rise and the present subtidal areas will become deeper (i.e. light limited), forcing seagrasses beds to migrate landward into shallower areas, such as the newly formed areas adjacent to retreating marshes (Kentula and McIntire 1986, Ehler et al. 1996). If these newly formed areas are not suitable, seagrasses will no longer be found in that area. In order to address this question, seagrass growth parameters as a function of sediment organic content were determined *in situ* and in a controlled experiment to test the hypothesis that old marsh peat is limiting seagrass productivity and distribution due to its relatively high organic content.

Species	Sediment type	Location	Reference
Amphibolis spp.	medium sand	Holdfast Bay, South Australia	Clarke 1987
Cymodocea nodosa	finer sediment than *P. oceanica*	Monteroso Bay, Italy	Cavazza et al. 2000
Heterozostera tasmanica	clay rich sediment	Western Port, Australia	Marsden et al. 1979
Posidonia oceanica	medium sand	Holdfast Bay, South Australia	Clarke 1987
Posidonia oceanica	coarse, medium grained sand	Monteroso Bay, Italy	Cavazza et al. 2000
Posidonia oceanica	muddy sand	Gulf of Oristano, Sardinia, Italy	De Falco et al. 2000
Posidonia sinuosa	fine sand and medium sand mix	Shoalwater Bay, Western Australia	van Keulen and Borowitzka 2003
Phyllospadix spp.	Mudstone substrate	San Diego County, California, USA	Stewart 1989
Ruppia maritima	silt/clay mix	Severn River, Maryland, USA	Arnold et al. 2000
Thalassia testudinum	calcareous mud overlaying autochthonous peat	Biscayne Bay, Florida, USA	Zieman 1972
Thalassodendron ciliatum	Sand	Inhaca Island, Mozambique, Africa	Bandeira 2002
Thalassodendron ciliatum	Pleistocene calcareous sandstone	Inhaca Island, Mozambique, Africa	Bandeira 2002
Thalassodendron pachyrhizum	Sand-covered or bare limestone	Shark Bay to the Great Australia Bight, Australia	Kirkman and Cook 1987
Zostera muelleri	clay rich sediment	Western Port, Australia	Marsden et al. 1979
Zostera noltii	Sand	Dutch Wadden Sea, The Netherlands	Philippart and Dijkema 1995

Table 1: Sediment types in various seagrass habitats around the world.

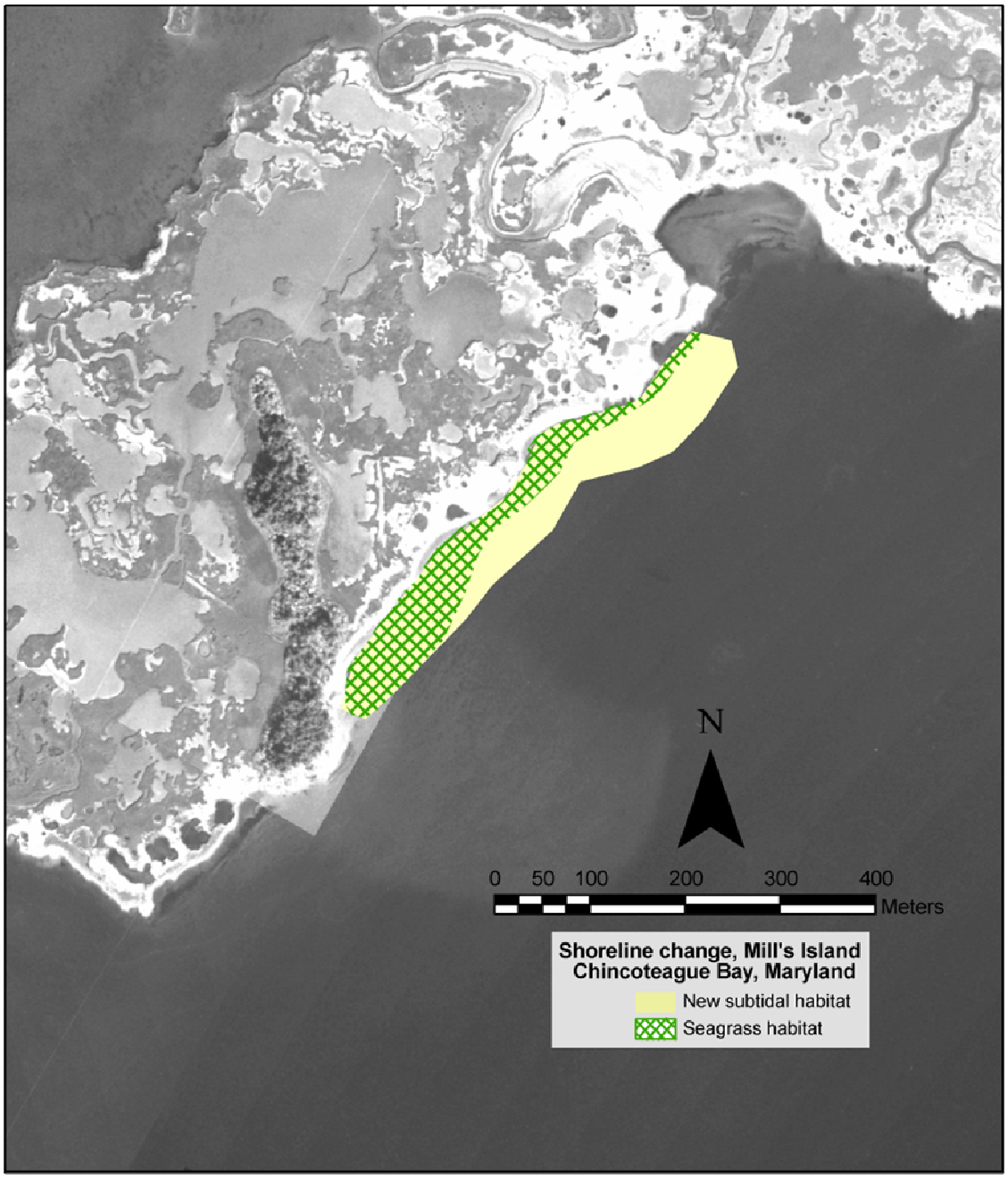


Figure 1: Potential seagrass habitat at Mill's Island, Chincoteague Bay. The yellow area represents the newly available seagrass habitat based on an erosion rate of 0.60 m y^{-1} for the last 100 years, i.e. marsh area lost in the last 100 years. The green hatched area represents current depths ≤ 1 m, which is considered the maximum depth for seagrass distribution at Mill's Island. Therefore, the hatched area represents the extent of the area where seagrasses can exist at present.

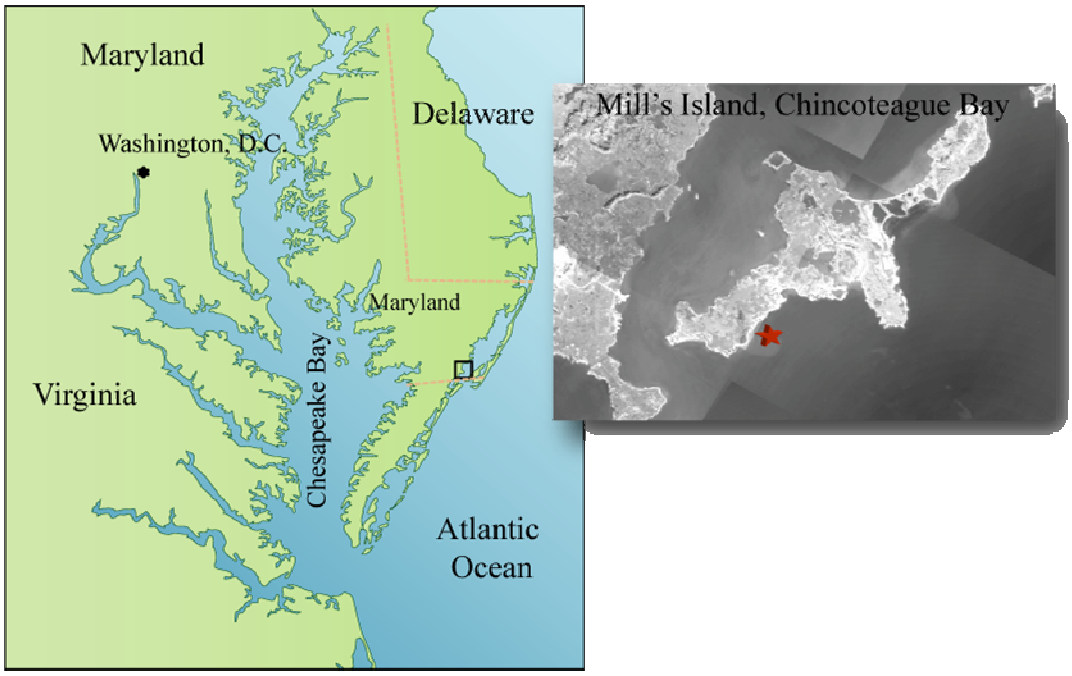
METHODS

Study site

Mill's Island in Chincoteague Bay (Figure 2) was selected based on the presence of a retreating marsh shoreline with an adjacent seagrass bed. The present study took place at the southeast portion of the island, along a beach extending southwest to northeast. The substrate in the seagrass habitat (i.e. < 1 m water depth) was dominated by old marsh peat along the northeast shoreline and seagrass beds were absent, while the substrate in the seagrass habitat was dominated by a thin sand layer over old marsh peat along the southwest shoreline and seagrass were present (Figure 3). The source of sand was an eroding dune within the marsh system (Figure 3). As the marsh ended in the form of an abrupt scarp, the distance between the erosional marsh shoreline and the shallow edge of the seagrass bed was less than 20 meters. The astronomical tidal range at the site was less than 30 cm (NOAA 2005).

Light availability

Due to a well established *Zostera marina* bed at the study site, it can be assumed that seagrass light and water quality requirements are met. In order to assure that shoreline erosion was not increasing turbidity near shore and therefore affecting the results, the geographical variability of light availability was determined on July 6, 2004. Measurements were taken close to mid-day while the weather was windy and sunny. Light measurements and GPS coordinates were taken at five points along each of ten transects that ran perpendicular to the shoreline. This ensured that the entire area where seagrasses could be growing along the southeast side of Mill's Island was covered. A 4π light sensor (LI-COR, LI-193) was connected to a datalogger (LI-COR, LI-1400) and



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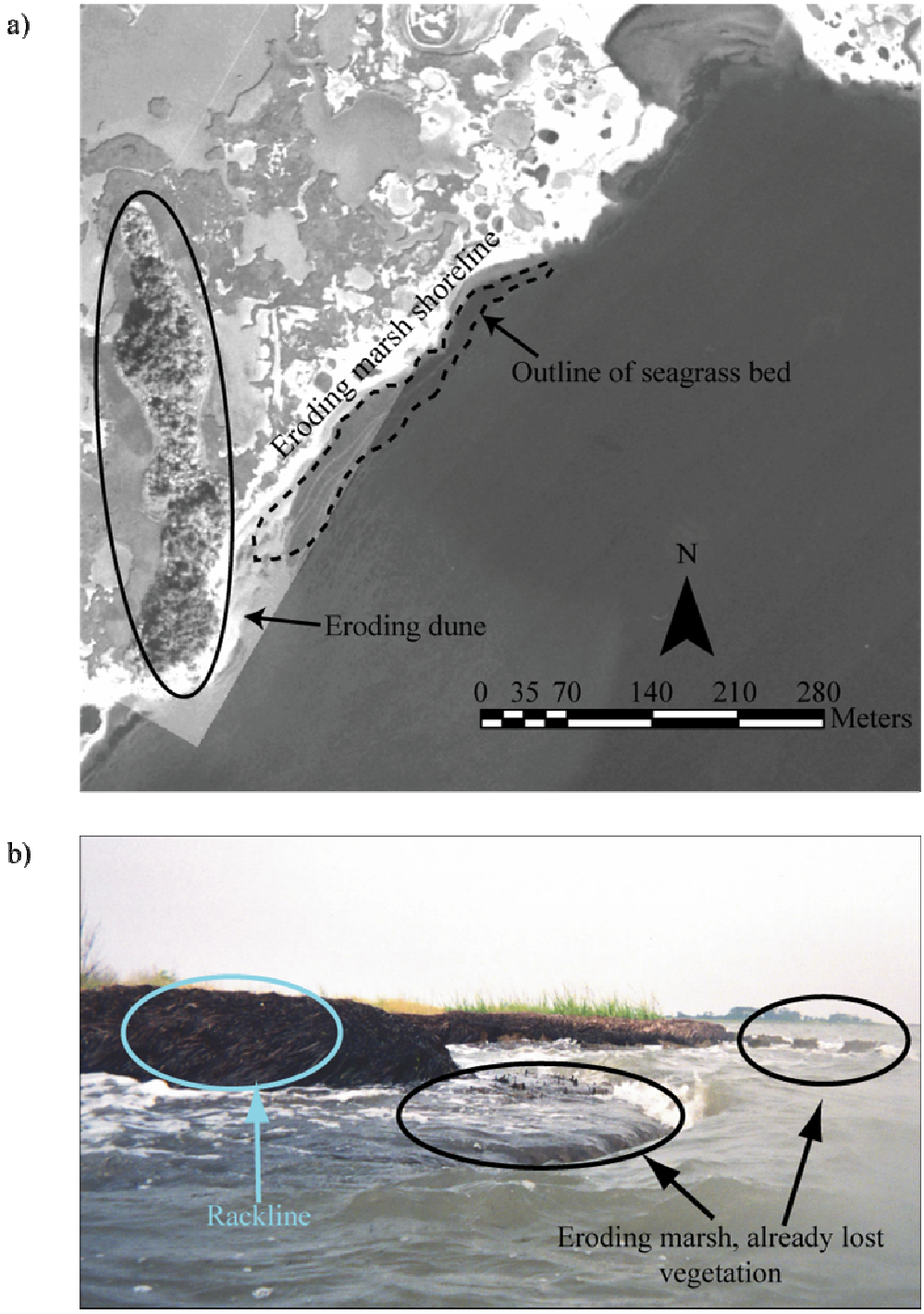


Figure 3: Location of the *Zostera marina* bed and eroding Pleistocene dune at Mill's Island. Chincoteague Bay. Maryland (a). Edge of the seagrass bed was determined by visually assessing a 2003 aerial photograph (courtesy of VIMS) for change in color between bed and bare sand. Photograph of eroding marsh shoreline at Mill's Island (b). Note the process of marsh retreat: marsh erodes from top and edge forming unvegetated platforms that continue to erode until flush with the seafloor.

light was measured in μmol photons m^{-2} s^{-1} at 0.20 m below the surface (I_o) and at a deeper depth, up to 1.4 m (I_z). The light attenuation coefficient (K_d) was calculated using the Lambert-Beer equation:

$$K_d = [-\ln (I_o/I_z)]/z$$

where I_o is the light just below the surface, I_z is the light at depth (z) and z is the difference in depth between I_o and I_z. The average light attenuation coefficient ± standard error was calculated for all depths, depths ≤ 1.0 m and depths > 1.0 m. Using Surfer 8.00 Surface Mapping System (Golden Software, Inc.), a spatial representation of the light attenuation coefficient adjacent to Mill's Island was generated.

Field surveys

In July and August 2004, the waters off the SE shore of Mill's Island were surveyed for seagrass distribution along two transects. Surveys and aerial photographs showed the seagrass bed to be narrow and to follow the shoreline. The outer transect started at the base of the erosional dune and ran northeast, ending beyond the edge of the seagrass bed (Figure 4). This transect length was 340 m and covered the southwest and northeast edges of the seagrass bed. The inner transect was parallel to the outer transect but 20 m closer to shore (Figure 4). The inner transect was 320 m long, covered the entire length of the seagrass bed and ended at the edge of the marsh. Along each transect, GPS coordinates (Garmin International, Inc. eTrex, ± 3 m), water depth (meter stick), seagrass species and shoot density (25 x 25 cm quadrat) were quantified every 10 m. Sediment samples (core = 5 cm in diameter) were also taken every 10 m to determine the thickness of the sand overlaying the old marsh peat. Using the same cores, additional sediment samples were collected every 20 m. The sand and old marsh peat layers in

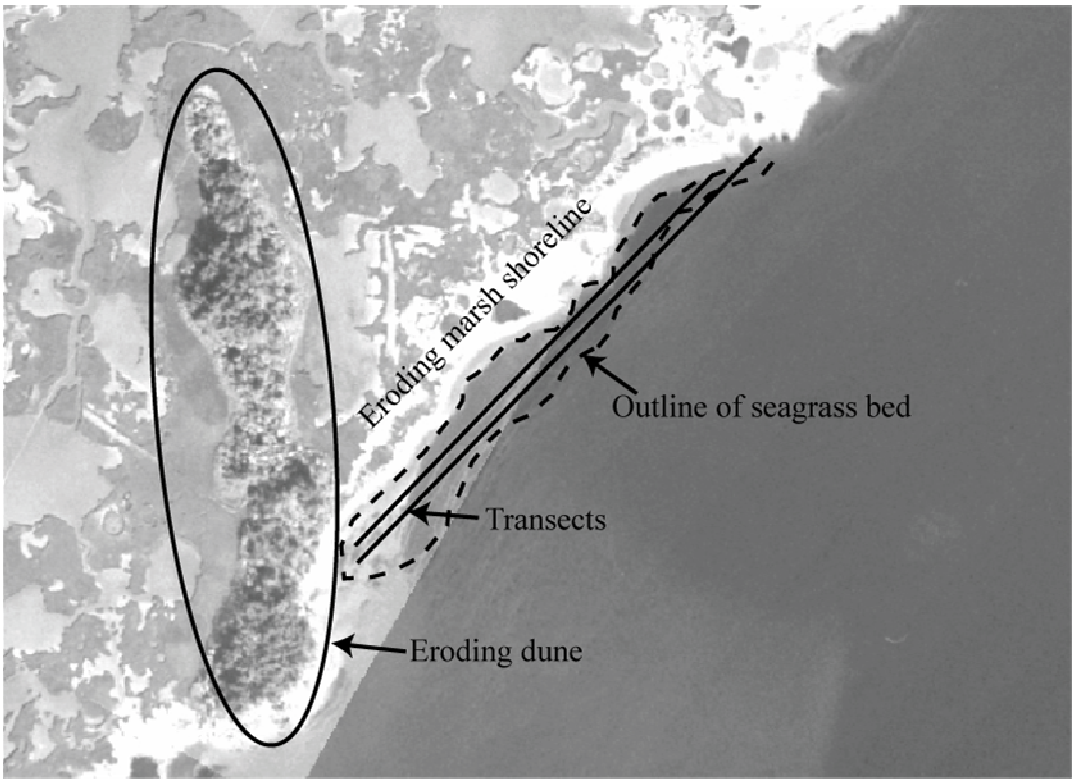


Figure 4: Transect lines for the 2004 survey of a *Zostera marina* bed at Mill's Island, Chincoteague Bay, Maryland. The 2005 survey followed the 80 cm depth contour in proximity of the 2004 inner transect.

these cores were separated based on differences in grain size and sediment color, with the sand having a higher percentage of large grain sizes than the old marsh peat. The different layers were then put in separate, labeled plastic bags and taken to the lab for characterization of grain size and organic matter content according to Erftemeijer and Koch (2001).

In order to determine the relationships between plant biomass, leaf and root length and sediment organic matter, seagrass samples were taken at pre-selected locations along each transect in late October, 2004. These locations represented the range of sediment (sand, old marsh peat and sand overlaying old marsh peat) and seagrass shoot density (vegetated and unvegetated) combinations found at Mill's Island (Table 2). At each location, three samples of seagrasses were collected with a 5 cm-diameter core within 50 cm of where sediment cores were taken during the previous summer and combined into one sample per location. Prior to combining samples in one bag, all plant material was rinsed in seawater in a sieve to remove any sediment attached to the roots and rhizomes. Samples were refrigerated (6˚ C) until leaf and root length were measured (within 4 wks) via direct measurement using a ruler. Once length measurements were complete, samples were placed in a drying oven (50˚ C), dried to constant weight and weighed to determine biomass.

In June 2005, the field survey was repeated to gather more detailed data on the relationship between plant biomass, leaf and root length and sediment characteristics. While the previous year's data showed a possible relationship between plant growth parameters and sediment organic content, there were not enough samples to make a definitive statement about whether sediment organic content in sediments adjacent to

Inner Transect	
Sand layer depth	Seagrass Present?
> 30 cm	Yes
> 30 cm	No
< 10 cm	Yes
< 10 cm	Yes
Outer transect	
Sand layer depth	Seagrass Present?
> 25 cm	No
> 20 cm	Yes
> 20 cm	Yes
20 cm	Yes
5 cm	No
0 cm	No

Table 2: Description of locations chosen for biomass sampling at Mill's Island in 2004.

retreating marshes is limiting seagrass growth. However, instead of two straight transects through the seagrass bed, fifteen points along a transect at the 80 cm depth contour were sampled, thereby eliminating depth as a co-variable. Seagrass and sediment samples were collected and processed the same way as in the previous year. However, the three seagrass samples taken at each location were kept separate as subsamples rather than combining all into one sample.

Due to the difficulty in comparing seagrass growth parameters to sediment organic content in layered sediments, an organic content value for the top 15 cm of sediment was estimated for each sampling location, which was the rhizosphere of the plants and was based on maximum root lengths from 2004 and 2005. The equation used was:

$$OC_{est} = (F_s \times OC_s) + (F_{omp} \times OC_{omp})$$

where OC_{est} was the weighted estimate of sediment organic content, F_s was the fraction of the top 15 cm of sediment that was sand, OC_s was the organic content of the sand, F_{omp} was the fraction of the top 15 cm of sediment that was old marsh peat and OC_{omp} was the organic content of the old marsh peat. Therefore, as sediment organic content values increased, actual samples changed from sand only to sand overlaying old marsh peat to old marsh peat only.

Sediment organic content experiment

An outdoor mesocosm (3.07 m long x 0.66 m wide x 0.60 m high, Figure 5) with extensive aeration for carbon dioxide supply and water movement was used to determine the response of *Zostera marina* to different sediment organic contents. Use of a single mesocosm containing all organic content treatments ensured that nutrients possibly being

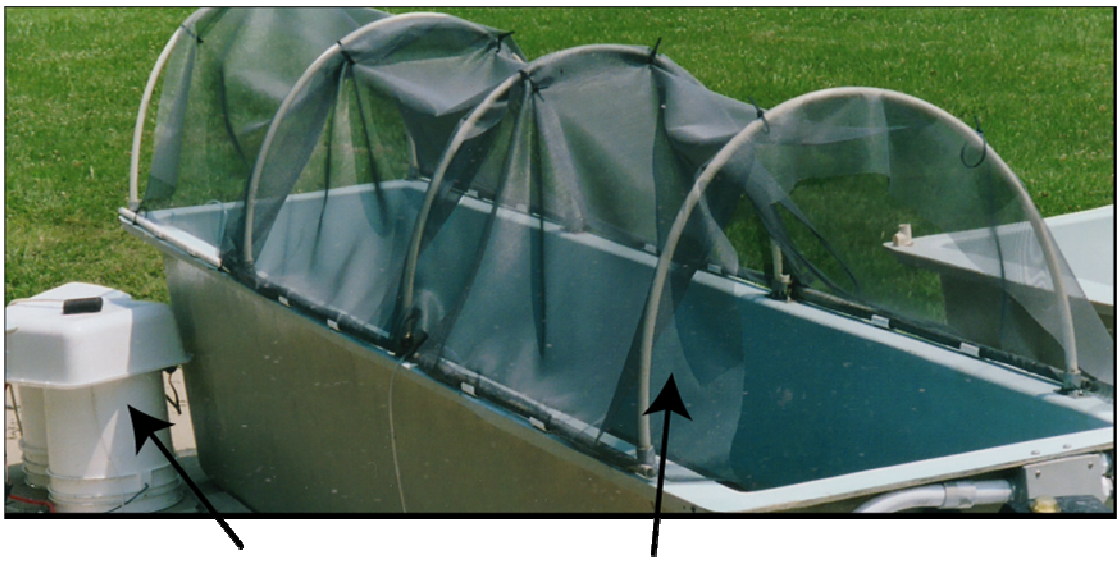


Figure 5: Outdoor mesocosm used for sediment organic content experiment. Screening helped to keep water temperatures and epiphytic loading low. Aerators (under buckets) provided carbon dioxide and water movement.

released from the sediments into the water column were well mixed, such that all plants, independent of the sediment they colonized, were exposed to the same water column nutrient concentrations. In order to obtain different organic contents, different types of sediments were mixed (Table 3). The degree of compaction of the experimental sediment was different for all treatments. However, the 4.4% organic treatment (100% old marsh peat) became an unconsolidated liquid when first mixed and therefore, it was left in its natural compacted state for the experiment. Three replicates of each treatment (0.1, 0.5, 1.2, 4.4, 5.9 and 10.3% organic content) were used, totaling 18 compartments, each 25 cm long x 19 cm wide x 10.5 cm deep (Figure 6).

First, the compartments were placed in an indoor annular flume in December 2004 to ensure equilibration of geochemical gradients in the sediments. The sediments were allowed to equilibrate in the compartments for two months under continuous water flow (10 cm s^{-1} at sediment surface) and 20˚ C. During this period the water (filtered Choptank River water, salinity = 10 to 15) was changed weekly. The compartments were then moved to the outdoor mesocosm in April 2005 for the start of the experiment. The mesocosm was covered with two layers of neutral density screening to prevent the water from excessive heating and to minimize epiphytic growth. Two air pumps (Optima, #807) provided carbon dioxide and water movement. Choptank River water was combined with Crystal Sea Marinemix (Marine Enterprise International) to raise the salinity to equal that of the collection site (salinity = 28) and a 50% water change occurred weekly. *Zostera marina* seedlings (single shoots) from Chincoteague Bay were planted in the compartments (4 plants $compartment^{-1}$) in April 2005 and were allowed to grow for eight weeks. Two weeks before the end of the experiment, leaves were punched

Treatment (% organic content)	Sediment Source 1	Sediment Source 2
0.1 ± 0.0	Beach dune sand[a]	—
0.5 ± 0.0	Marsh dune sand[b]	Old marsh peat[c]
1.2 ± 0.0	Marsh dune sand[b]	Old marsh peat[c]
4.4 ± 0.2	Old marsh peat[c]	—
5.9 ± 0.0	Old marsh peat[c]	Marsh sediment[d]
10.3*	Marsh sediment[d]	—

[a] Beach dune sand obtained from Assateague State Park
[b] Marsh dune sand obtained from Mill's Island, Chincoteague Bay, Maryland.
[c] Old marsh peat obtained from subtidal area adjacent to Mill's Island, Chincoteague Bay, Maryland.
[d] Marsh sediment obtained from Horn Point Marsh, Cambridge, Maryland. Sediment was a mixture of decomposed marsh vegetation and soil.
* Only one sample analyzed for organic content.

Table 3: Sources of sediment used to obtain a range of sediment organic content treatments for the mesocosm experiment.

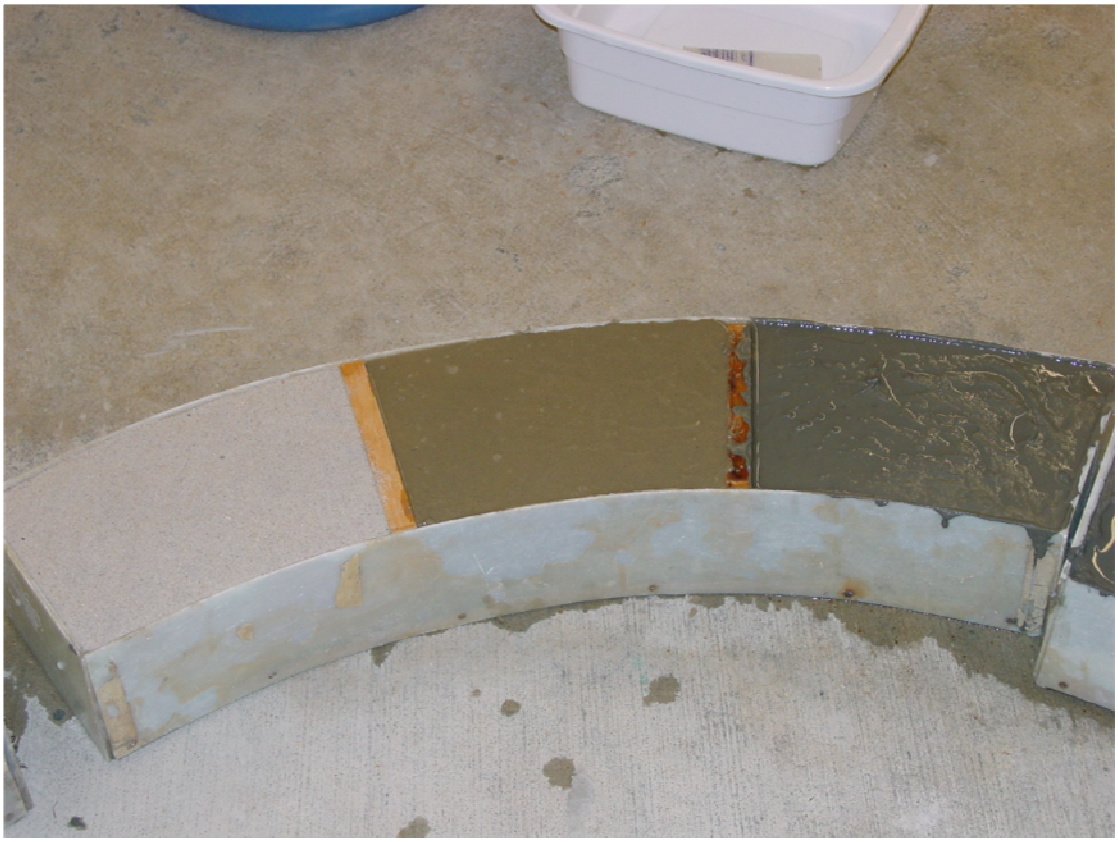


Figure 6: Compartments (25 cm long x 19 cm wide x 10.5 cm deep) with different sediments used for the organic content experiment an in outdoor mesocosm. Left to right: 0.1%. 1.2% and 4.4% organic content.

to determine growth rate and new biomass produced (Dennison 1990). At the end of the experiment, new growth, plant biomass and length (leaf and root) were determined.

Statistical analysis

Data from the sediment organic matter experiment was analyzed using analysis of variance (ANOVA, α=0.05) in SAS 9.1. Aboveground and belowground biomass was tested across treatments, with biomass being the dependent variable and sediment organic content the independent variable. Homogeneity of variance was checked using Levene's test (α=0.05). Graphical representation of the data and the Shapiro-Wilk's test for normality showed all parameters to be non-normal and were log transformed. Transformed data was normally distributed and homogeneity of variances for all data was met. If significant differences were found using one way ANOVA, then factors were tested using least squares method (α=0.05).

RESULTS

Light availability

Light attenuation coefficients for Mill's Island ranged from 1.23 m^{-1} to 3.52 m^{-1} with an average of 2.05 ± 0.05 m^{-1} (Figure 7). For locations where total depth ≤ 1.0 m, the average light attenuation coefficient was 1.85 ± 0.12 m^{-1} while for locations where total depth > 1.0 m, the average light attenuation coefficient was 2.08 ± 0.05 m^{-1}. The light attenuation coefficients were relatively low close to the shoreline and relatively high in an eddy offshore (Figure 7).

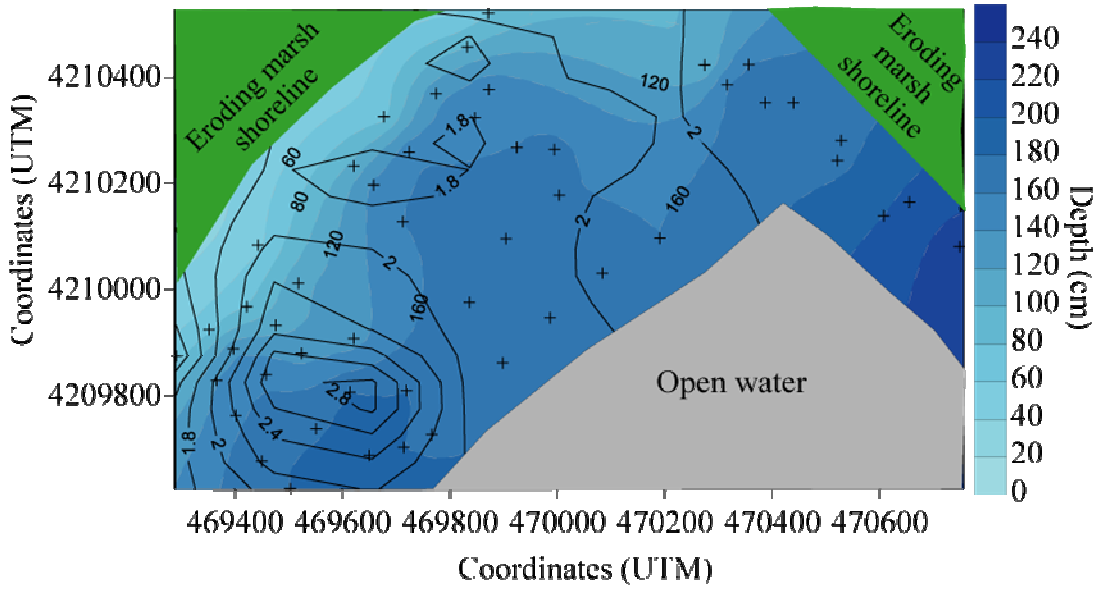


Figure 7: Light attenuation coefficients, K_d (m^{-1}), and water depth at Mill's Island on July 6, 2004. Light attenuation coefficients marked by contour lines, water depth by color and data points by "x's".

Field surveys

The grain size distribution of the sand at Mill's Island was dominated by fine sand (125 μM) and the old marsh peat by silt + clay (< 63 μM, Figure 8a). Samples that consisted of sand overlaying old marsh peat had a thin (≈ 1 cm) mixed layer between both sediment types (Figure 8a SEs). Sediment organic content increased as the proportion of silt + clay increased (Figure 8b).

Sampling along the outer transect in 2004 indicated no relationship between seagrass shoot density and sediment organic content, although shoot density decreased above 2% organic content (Figure 9a). However, water depth increased to above 1 m in the same area that density decreased (Figure 9b). Therefore, water depth was a co-determinant of shoot density along the outer transect. It was evident that water depth (i.e. light) was limiting seagrasses at the outer edge of the bed (Figures 7 and 9). Therefore, only the inner transect data will be discussed for 2004. Water depth was not a co-variable along the inner transect. Seagrass shoot density increased with increasing sediment organic content until ~3.5%, at which point density decreased as organic content continued to increase ($r^2 = 0.26$, Figure 10a). Biomass increased with increasing sediment organic content up to approximately 4.0% (Figure 10b). There was no relationship between average leaf and root length and sediment organic content (data not shown).

In contrast, in the following year, seagrass shoot density decreased with increasing sediment organic content ($r^2=0.38$, Figure 11a). Most sites (n=10) that had low organic content were vegetated, with shoot densities ranging from 0 to 587 shoots

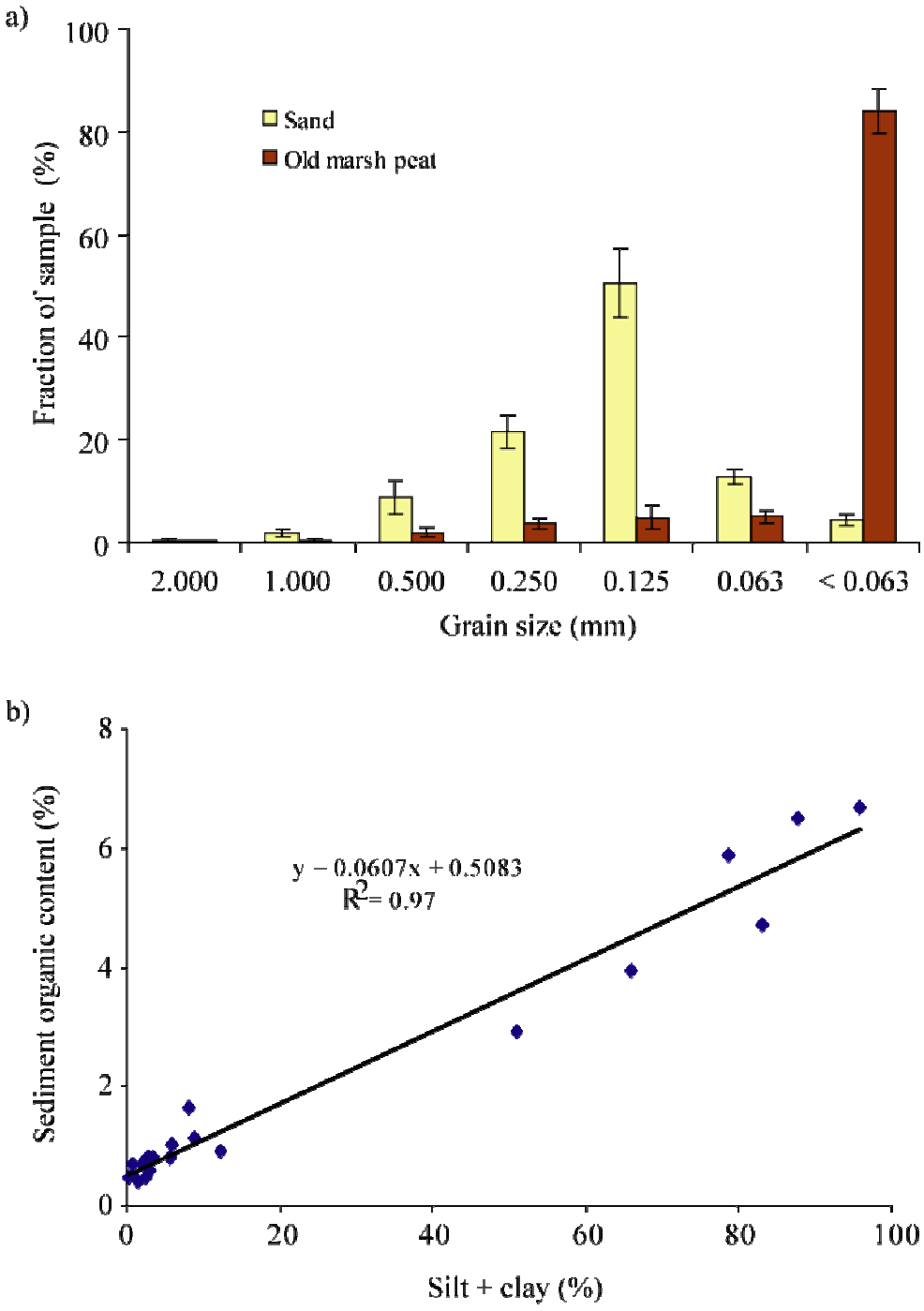


Figure 8: Grain size distribution of sand and old marsh peat at Mill's Island in 2004 (a). Vertical lines represent SE. Sediment organic content as a function of the silt + clay fraction (b).

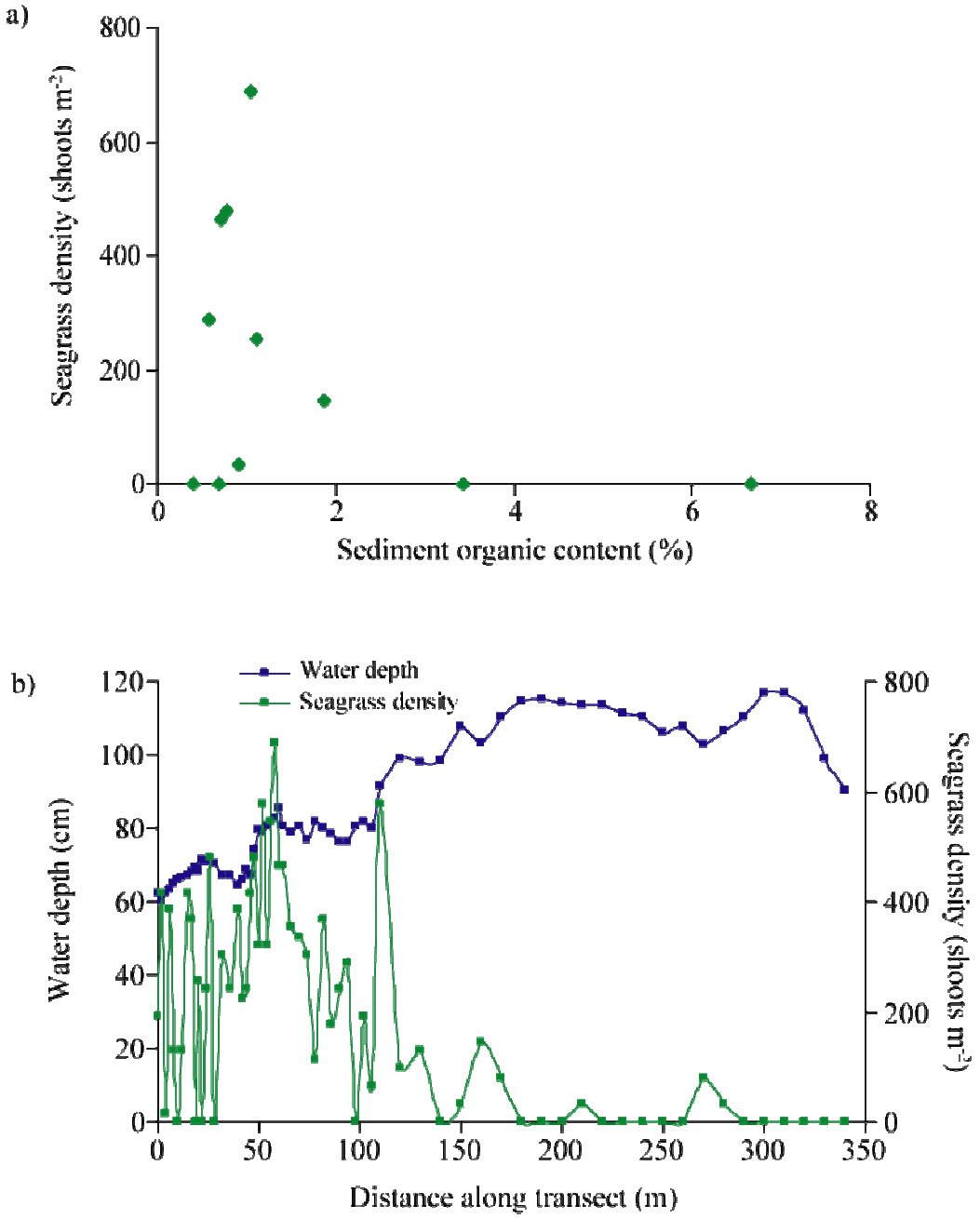


Figure 9: Shoot density of *Zostera marina* compared to sediment organic content in the rhizosphere (top 15 cm) along the outer transect at Mill's Island in 2004 (a). Water depth and seagrass shoot density along the outer transect (b). Note how seagrass shoot density decreases as water depth increases.

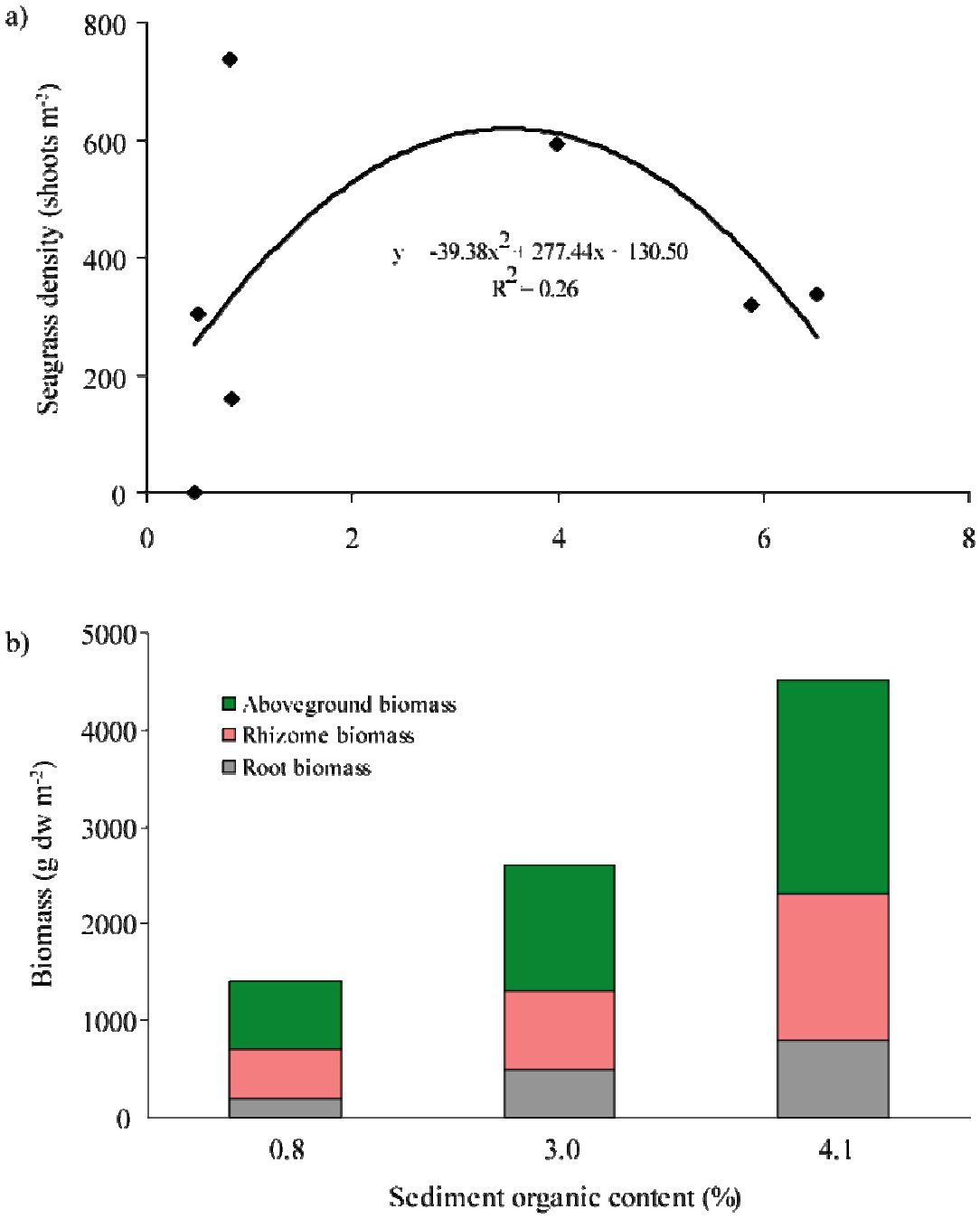


Figure 10: Shoot density (a) and biomass (b) of *Zostera marina* as a function of sediment organic content in the rhizosphere (top 15 cm) along the inner transect at Mill's Island in 2004.

m^{-2} (Figure 11b). Sites that had high organic content had lower shoot densities (0 to 43 shoots m^{-2}, n=3, Figure 11b). Average aboveground and belowground biomass decreased linearly with increasing sediment organic content (r^2=0.39, r^2=0.38 respectively, Figure 12). Average leaf and root length decreased with increasing sediment organic content (r^2=0.34, r^2=0.39 respectively), but maximum root length had no relationship with sediment organic content (Figure 13).

Sediment organic content experiment

The characteristics of the sediment in the high organic treatment (10.3%) were different than the other five treatments. The texture was a loam, rather than a sand or clay. The sediment was a mixture of sand, clay and decaying organic matter. Additionally, high amounts of iron minerals were observed (orange porewater and orange roots) in this treatment throughout the experiment, while no iron minerals were detected in any other treatment at any time during the experiment. This highly organic sediment never compacted, as the other sediments did, and remained in suspension throughout the experiment, which may have resulted in lower sulfide concentrations than the other treatments. Due to these characteristics, the relationship between seagrass growth parameters and sediment organic content in the 10.3% organic treatment affected the overall results and conclusions for the entire experiment. Therefore, results for all treatments as well as for only the five lower organic treatments, i.e. excluding the 10.3% organic content treatment, are presented.

In general, all growth parameters (aboveground biomass, belowground biomass, leaf length and root length) had a polynomial trend with sediment organic content, increasing up to 5.9% and declining thereafter, except the growth rate and the average

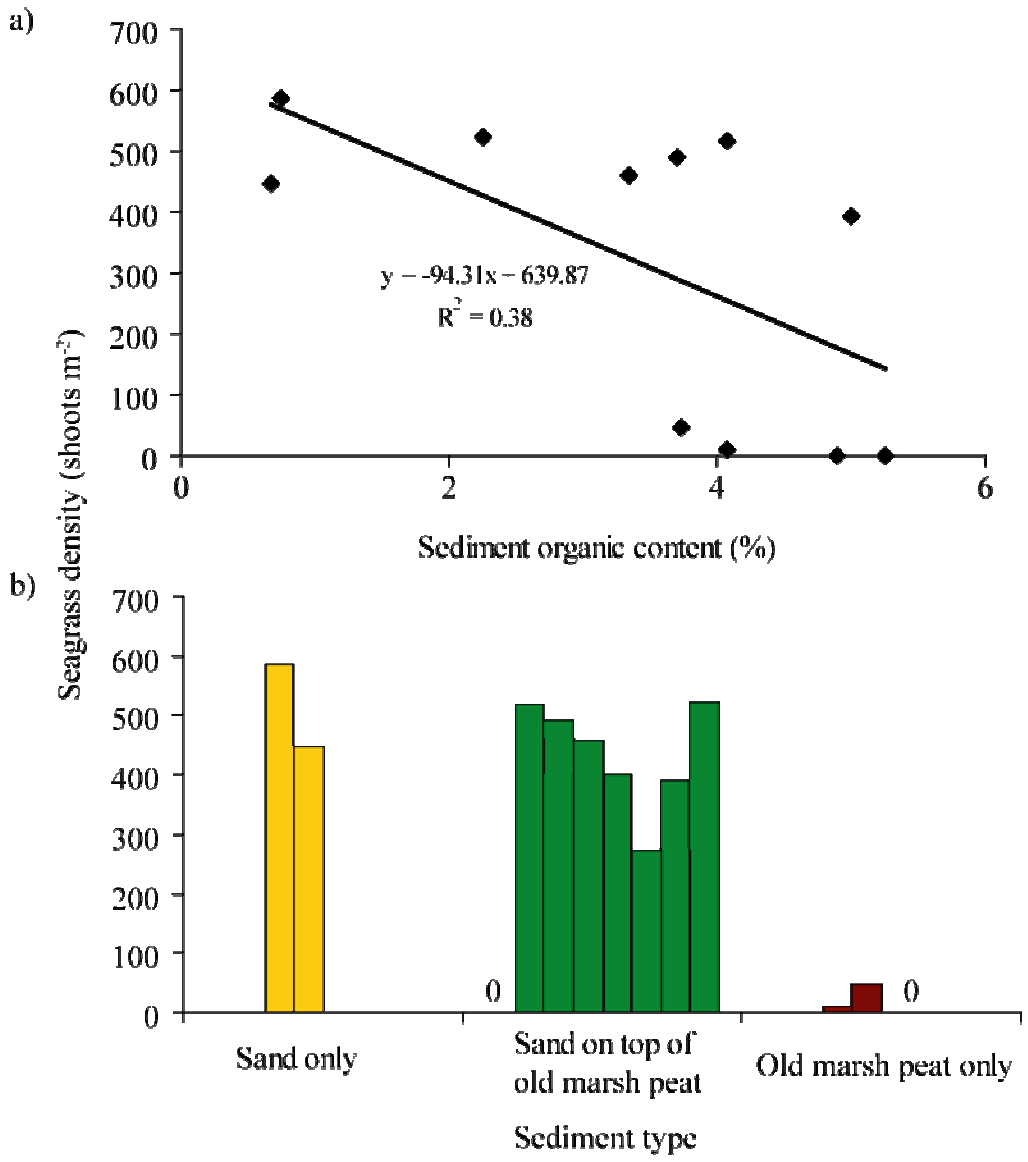


Figure 11: (a) Shoot density of *Zostera marina* as a function of sediment organic content in the rhizosphere (top 15 cm) at Mill's Island in 2005. (b) Shoot density can be grouped into low organic and high organic content sediment.

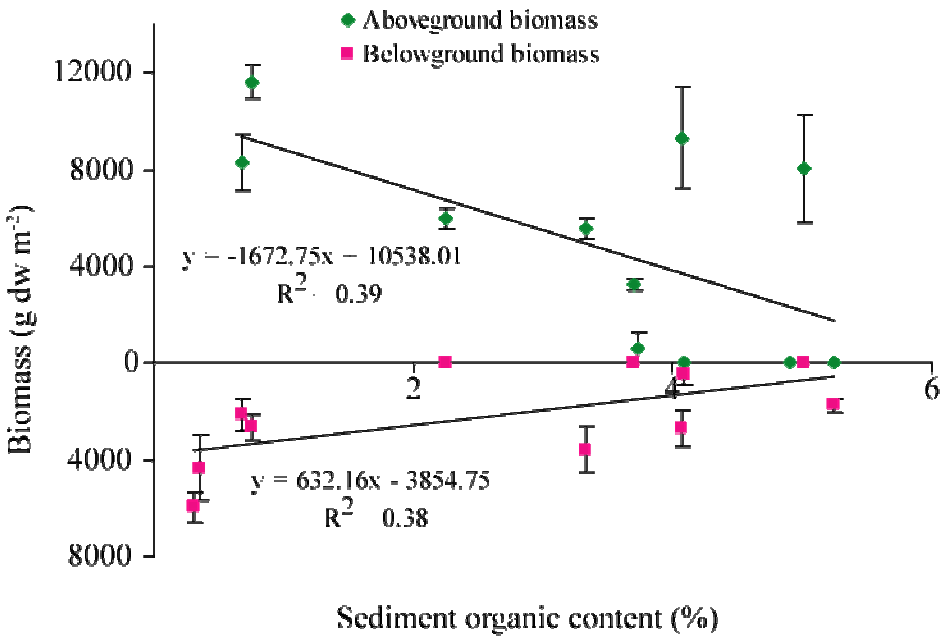


Figure 12: Average aboveground and belowground biomass of *Zostera marina* as a function of sediment organic content in the rhizosphere (top 15 cm) at Mill's Island in 2005. Vertical lines represent SE.

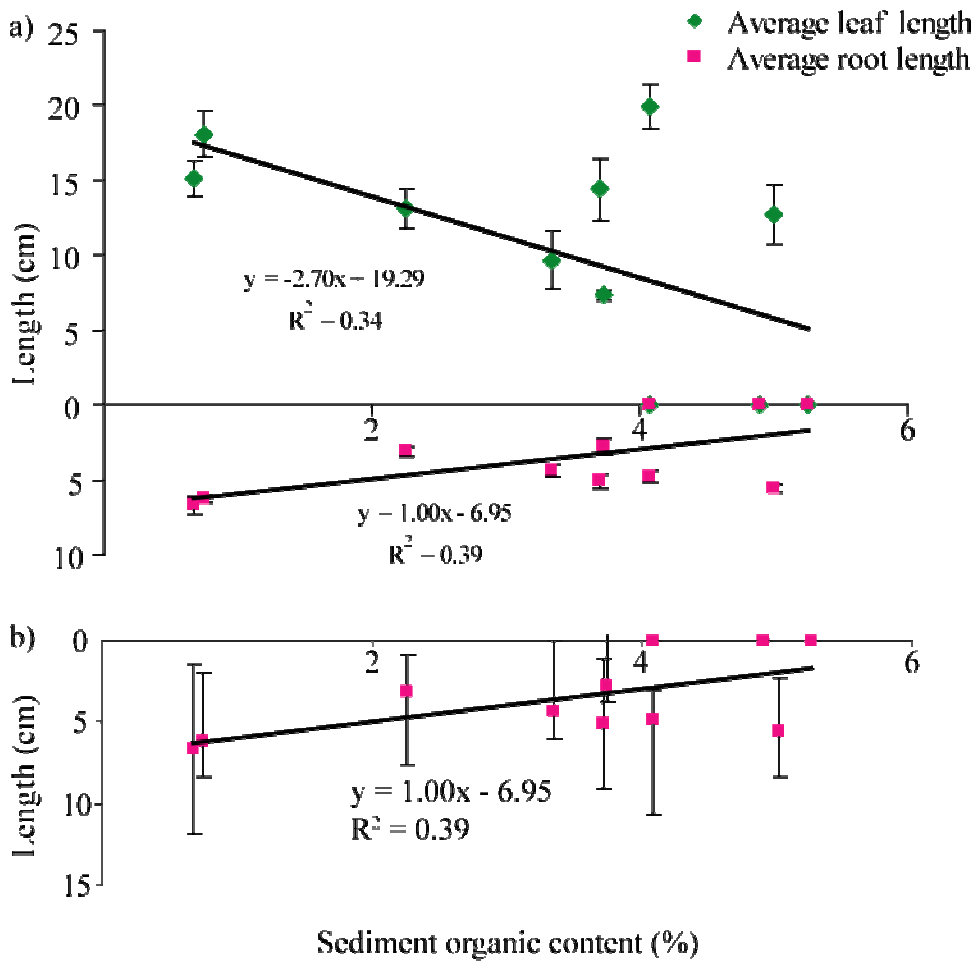


Figure 13: Average leaf and root length of *Zostera marina* as a function of sediment organic content in the rhizosphere (top 15 cm) at Mill's Island in 2005. Vertical lines in graph (a) represent SE while bars in graph (b) represent minimum and maximum root length.

leaf length:average root length, which showed positive linear trends up to 10.3% sediment organic content. Average aboveground and belowground biomass exhibited a trend with sediment organic content, increasing up to 5.9%, then decreasing thereafter (r^2=0.84, r^2=0.89, respectively, Figure 14a). When only organic contents up to 5.9% were considered, average aboveground and belowground biomass showed a positive linear trend with sediment organic content (r^2=0.84, r^2=0.91 respectively, Figure 14b). The growth rate expressed as new biomass (mg $shoot^{-1}$ day^{-1}) increased with increasing sediment organic content up to 10.3% (r^2=0.61, Figure 15a). Leaf elongation (i.e. growth) showed a positive linear trend up to 10.3% sediment organic content (r^2=0.75, Figure 15b). Average leaf length exhibited a trend with sediment organic matter, increasing up to 5.9% organic content, then decreasing thereafter (r^2=0.91, Figure 16a). When only organic contents up to 5.9% were considered, average leaf length exhibited a positive linear trend with sediment organic content (r^2=0.84, Figure 16b). Average root length showed a polynomial trend with sediment organic content (r^2=0.97, Figure 16a), but the relationship was forced by the highest organic content treatment (r^2=0.51, linear correlation, Figure 16b). The average leaf length to average root length ratio increased linearly with increasing organic matter (r^2=0.92, Figure 17).

There were significant differences ($p < 0.0001$) between sediment organic content treatments for aboveground and belowground biomass (Table 4). The aboveground biomass divided into two groups: (1) the 0.1% and 0.5% treatments were not significantly different from each other but significantly different from the four higher organic content treatments and (2) the 4 higher organic treatments were not significantly different from each other. The belowground biomass divided into three groups: (1) the 0.1%, 0.5% and

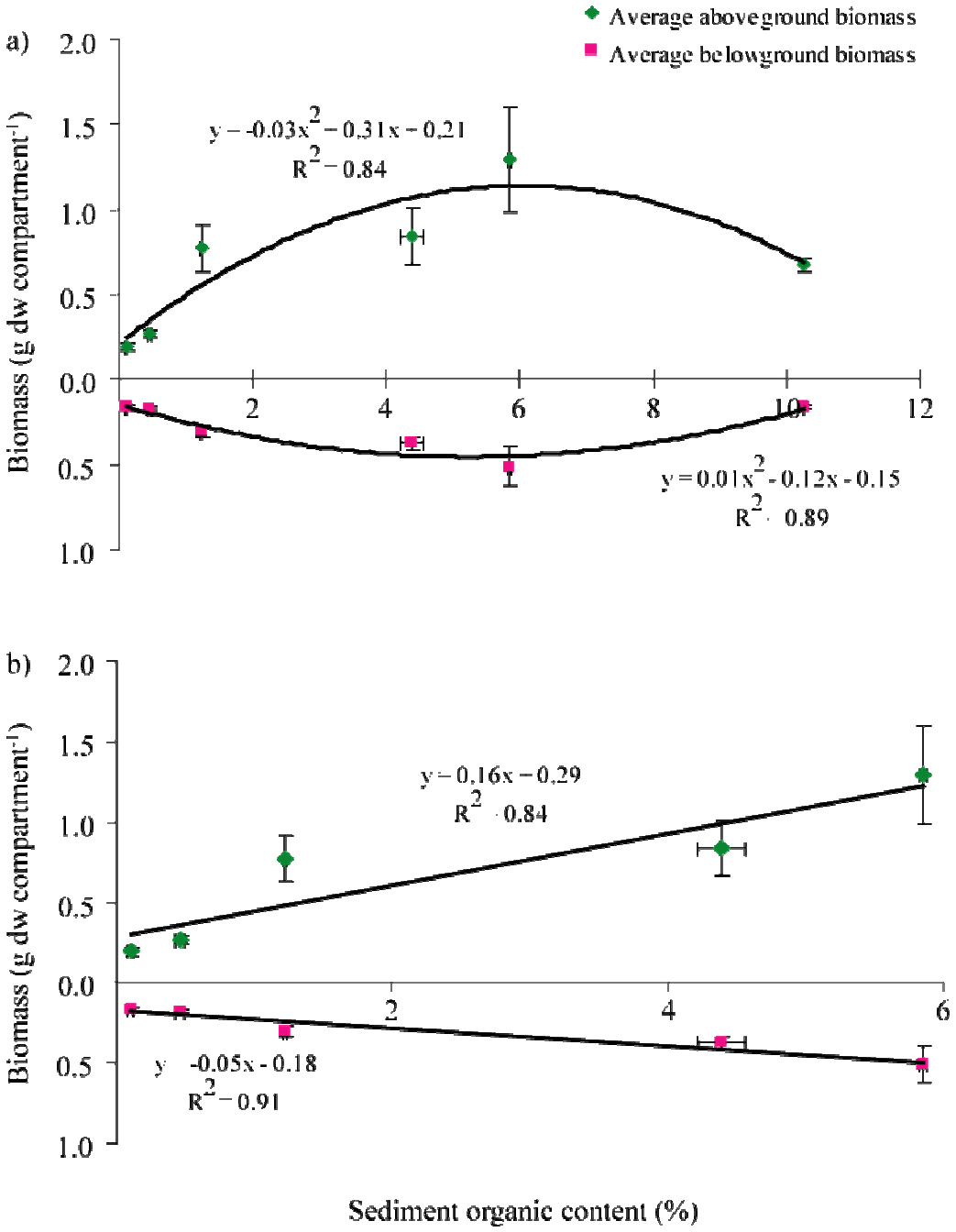


Figure 14: Average aboveground and belowground biomass of *Zostera marina* grown in sediments with organic contents between 0.1% and 10.3% in a mesocosm experiment (a). Seagrass biomass as a function of sediment organic contents between 0.1% and 5.9% (b). Horizontal and vertical lines represent SE.

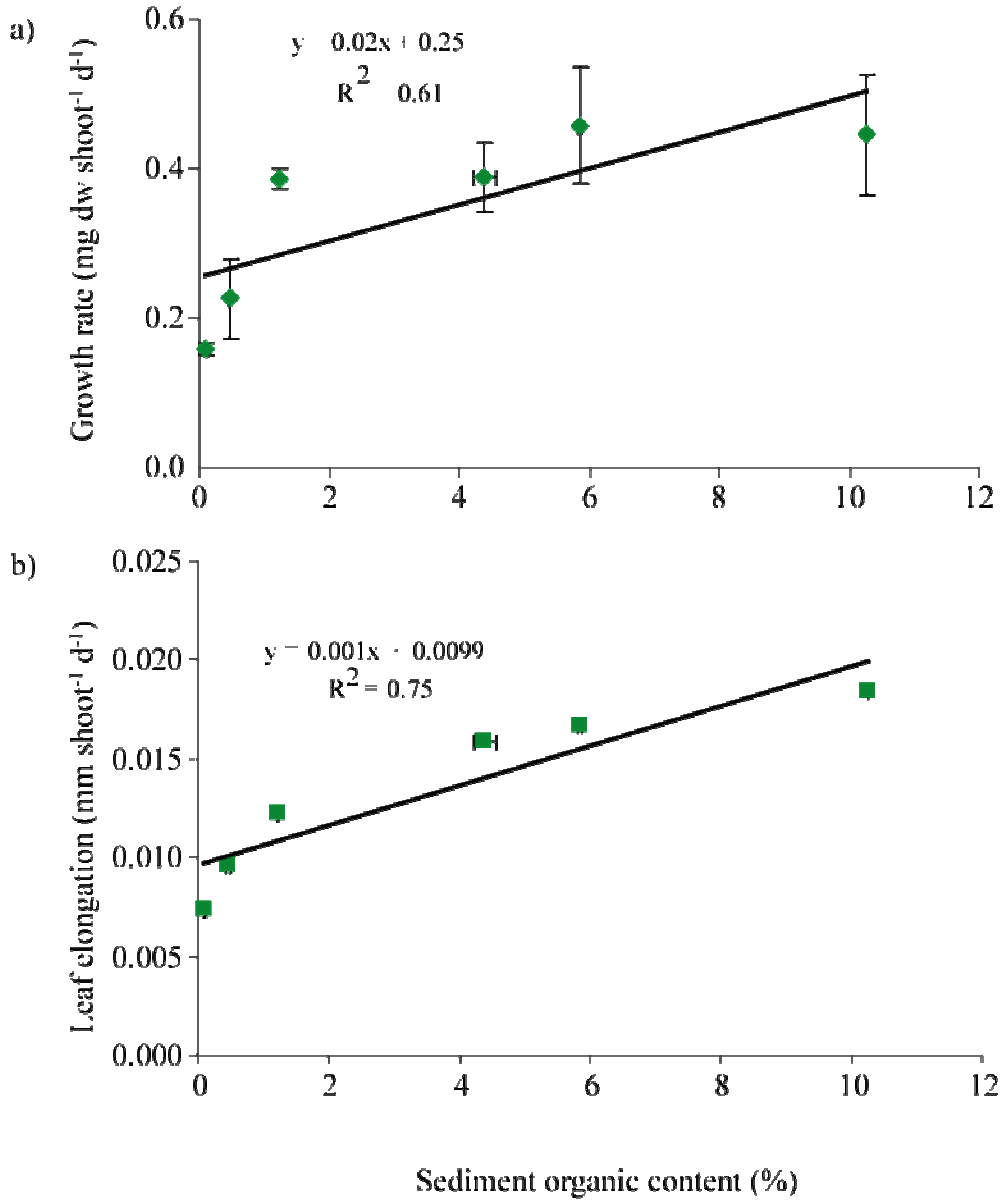


Figure 15: Growth rate of *Zostera marina* grown in sediments with different organic contents in an outdoor mesocosm experiment (a). Leaf elongation of *Zostera marina* in same experiment (b). Vertical lines represent SE of growth rate (graph a) and horizontal lines represent SE of sediment organic content (both graphs).

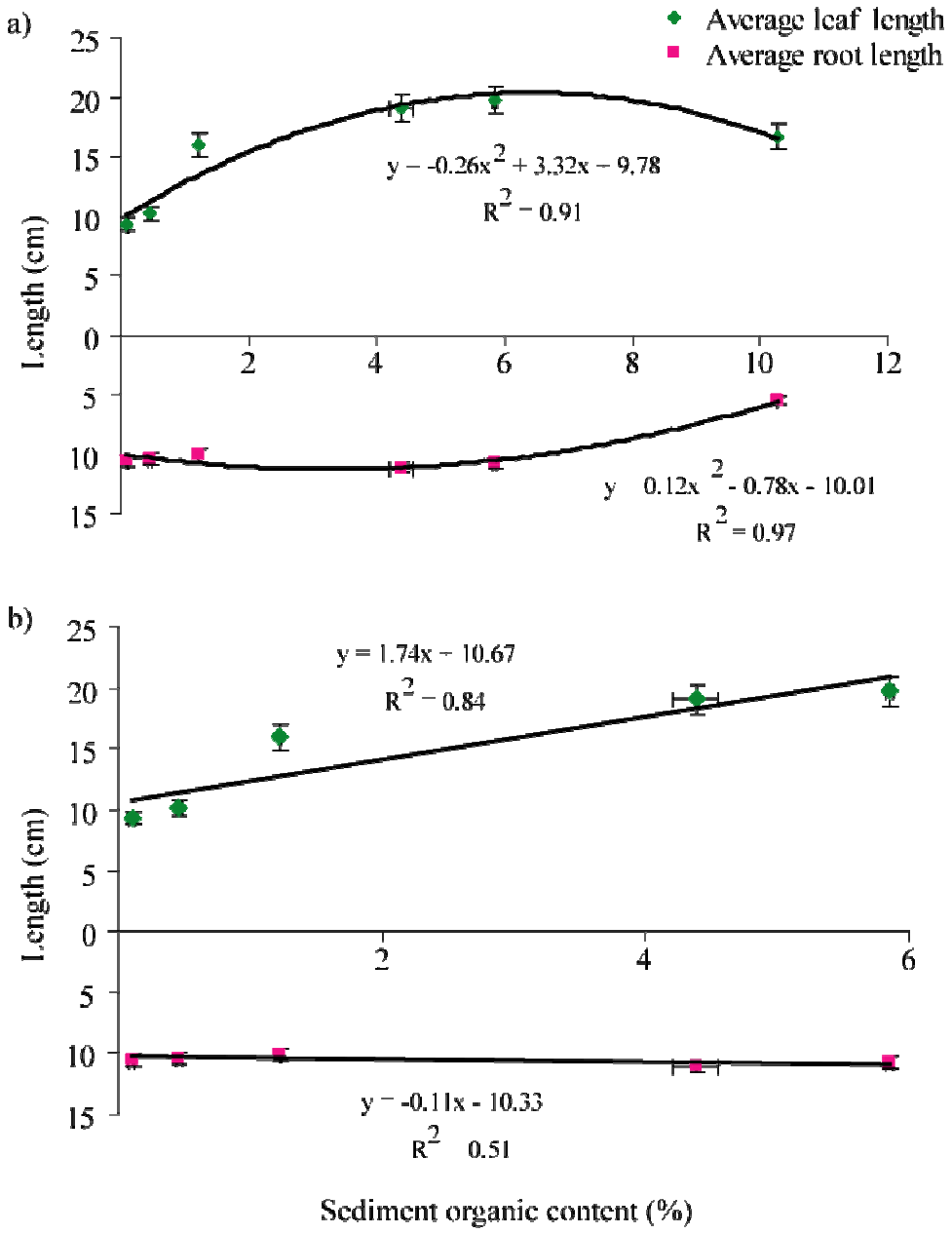


Figure 16: Average leaf and root length of *Zostera marina* grown in sediments with different organic contents in an outdoor mesocosm experiment (a). Sea-grass leaf and root length as a function of sediment organic contents between 0.1% and 5.9% (b). Horizontal and vertical lines indicate SE.

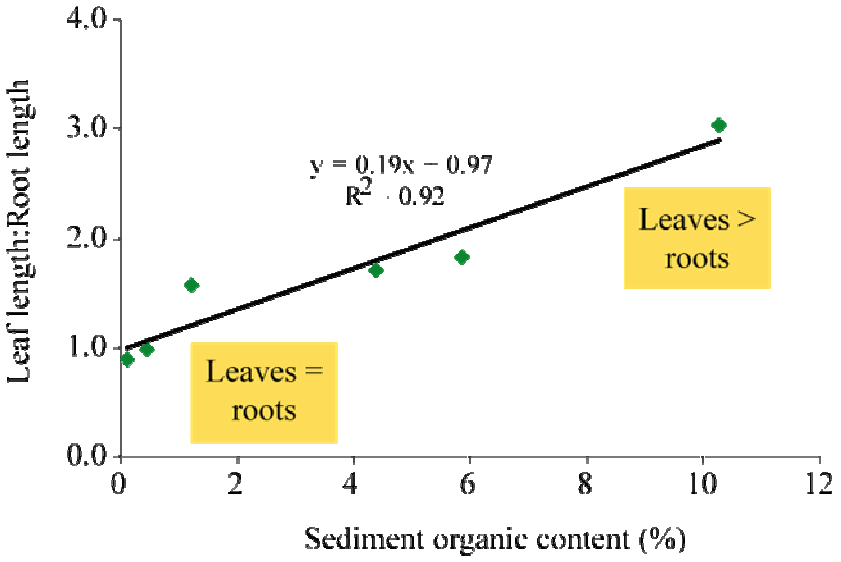


Figure 17: The ratio of average leaf length to average root length of *Zostera marina* grown in sediments with different organic contents in an outdoor mesocosm experiment.

Aboveground Biomass

Source of variation	df	Mean square	F value	P value
Organic matter	5	0.2376	6.45	<0.0001
Residuals	12	0.0369		
Total	17			
Transform	Ln (x+1)			
Levene's test	0.1176 (ns)			

Pairwise comparison

Rank of the means	1	2	3	4	5	6
Sediment organic content	0.1%	0.5%	1.2%	4.4%	5.9%	10.3%
Log transformed sediment organic content means	-0.7202	-0.5724	-0.1271	-0.0967	0.0881	-0.1723

a

b

Belowground Biomass

Source of variation	df	Mean square	F value	P value
Organic matter	5	0.1243	11.94	<0.0001
Residuals	12	0.0104		
Total	17			
Transform	Ln (x+1)			
Levene's test	0.1532 (ns)			

Pairwise comparison

Rank of the means	1	2	3	4	5	6
Sediment organic content	0.1%	0.5%	1.2%	4.4%	5.9%	10.3%
Log transformed sediment organic content means	-0.7819	-0.7606	-0.5176	-0.4321	-0.3048	-0.7848

a

b

c

Table 4: One way ANOVA ($\alpha = 0.05$) and pairwise comparisons for aboveground and belowground biomass in the controlled mesocosm experiment. Lines signify means that are not significantly different at the $p = 0.05$ level.

the 10.3% organic content treatment were not significantly different from each other, (2) the belowground biomass in the 0.5% and the 1.2% organic content treatment were not significantly different from each other and (3) the belowground biomass in the 1.2%, 4.4% and 5.9% organic content treatments were not significantly different from each other ($p = 0.05$). See Table 4 for all pairwise comparisons.

DISCUSSION

While high water column turbidity can be associated with erosional shorelines (Cronin and Langland 2003), this was not the case at the field site. There were eddies with higher turbidity water, but these seem to be transported along the shore (Figure 7), only temporarily decreasing light availability to seagrasses. The light attenuation coefficient for depths ≤ 1.0 m (i.e. seagrass habitat) at the study site (1.85 ± 0.12 m^{-1}) is close to the light attenuation coefficient requirement determined for *Zostera marina* in the Chesapeake Bay (1.5 m^{-1}, Dennison et al. 1993, Batiuk et al. 2000). While *Zostera marina* grew to a depth of 1.15 m at the site (Figure 9b), shoot density decreased with increasing water depth along the outer transect. In conclusion, light was limiting at the outer edge of the bed where water depth exceeded 1 m. In contrast, the presence of seagrasses adjacent to the erosional marsh confirms that light at depths < 1 m is suitable at the site, despite the marsh erosion. Therefore, other seagrass limiting factors need to be considered.

The mesocosm experiment showed that a minimum amount of organic matter is needed in the sediment so that *Zostera marina* growth is not inhibited by low amounts of nutrients. The availability of porewater ammonium (22% extractable NH_4) and low

porewater ammonium concentrations (~ 40 – 110 μM) in organic poor sediments have previously been shown to inhibit seagrass growth (Short 1987, Terrados et al. 1999). The pairwise comparison of the aboveground biomass in the mesocosm experiment shows that aboveground biomass may plateau above approximately 1% sediment organic content. Additionally, the significant difference between the low organic content treatments (0.1% and 0.5%) and the high organic content treatments (1.2% and greater) suggest that a minimum organic content requirement may also exist.

There appears to be a wide range of sediment organic contents that seagrasses can grow in and sediment organic content thresholds may be region specific. For example, *Zostera marina* is found growing in sediments with an organic content of 9.93% at a site near Fyn, Denmark (Holmer and Laursen 2002), but a more typical organic content for organic rich sediments in *Zostera marina* beds is around 3% (Holmer and Laursen 2002, van Katwijk and Wijgergangs 2004). Comparing the mesocosm results with these studies shows that, although not frequently found in nature, *Zostera marina* can grow in organic rich (above 3%) sediments.

Furthermore, the mesocosm experiment does not conclusively show that *Zostera marina* growth decreases above approximately 6% sediment organic content. While the pairwise comparison showed that belowground biomass in the 10.3% organic content treatments was significantly lower than the belowground biomass in the 1.2%, 4.4% and 5.9% organic content treatments, the 10.3% organic treatment was not ideal for this growth experiment. High levels of oxidized iron were noted in this treatment, evidenced by orange porewater and orange tinged roots. While dissolved iron is not known to be toxic to plants (Heijs et al. 1999), it has been shown to limit seagrass growth in carbonate

sediments (Duarte et al. 1995). Additionally, iron minerals, such as those found in the root zones of aquatic plants, are known to create plaques on the roots of plants (Zhang et al. 1999). Furthermore, iron hydroxides bind phosphorus, possibly decreasing the amount of P in the plant tissue (Christensen and Wigand 1998).

Additionally, the 10.3% organic content sediment had higher water content and higher amounts of refractory detritus than the other treatments, which may be negatively affecting growth. Growth was still higher in this treatment than the low organic treatments (< 1%), suggesting that even if there is a detrimental effect in organic rich sediments, plants will grow better than in organic poor (<1.0%) sediments. Regardless of the possible causes of the apparent decreased growth in the high organic treatment, seagrasses grew well in treatments where the sediment organic content equaled or exceeded the sediment organic content of old marsh peat (4.4%). Therefore, the sediment organic content of sediments adjacent to retreating marshes is not limiting to seagrass productivity and distribution.

Although sediment organic content did not limit seagrass growth parameters, it had an effect on the morphology of the plants in the mesocosm experiment. While leaf length increased with increasing sediment organic content, root length did not show a proportional increase, leading to plants with long leaves and short roots in high organic sediments. Since belowground biomass did increase with increasing sediment organic content, sediment organic content was not limiting belowground growth. Rather, root biomass was concentrated in the top 5 cm of the organic rich sediment, suggesting that sufficient resources (e.g. nitrogen and phosphorus) were available and roots did not have to become longer to acquire more resources. This relationship between plant morphology

and sediment type has been found in other studies on seagrasses. *Thalassia testudinum* growing in low porewater ammonium (~30 μM) sediments (i.e. low organic content) has significantly shorter and narrower leaves than *T. testudinum* growing in high porewater ammonium (~100 μM) sediments (i.e. high organic content, Lee and Dunton 2000). Additionally, when plants growing in low organic content sediments are fertilized, they increase in aboveground biomass but not belowground biomass, resulting in a significant difference in the ratio of aboveground to belowground biomass between fertilized and unfertilized plots (Lee and Dunton 2000). *Zostera marina* growing in Alaska has narrower leaves and increased amounts of root hairs in sandy sediments (i.e. low organic content), suggesting leaf and root morphology are related to nitrogen availability in sandy sediments (Short 1983). This relationship is absent in high nitrogen, muddy sediments. Instead, while *Zostera marina* plants are larger in muddy sediments than in sandy sediments, there are less root hairs (Short 1983). These studies help to explain the findings from the mesocosm experiment by suggesting that plants growing in different sediment types have different morphologies.

The relationship between sediment organic content and plant growth parameters in the mesocosm experiment was not supported by the findings *in situ*. While in the mesocosm seagrass growth increased with sediment organic content, *in situ* seagrass growth decreased with increasing sediment organic content, although the trends were not as strong (r^2 ranged from 0.34 to 0.51). One possible cause for the conflicting results is the high energy environment at Mill's Island (exhibited by the shoreline erosion). A possible factor influencing the presence/absence of seagrasses in old marsh peat may be that the plants in this type of sediment are morphologically unsuitable for high energy

environments. As seen in the mesocosm, plants growing in organic rich sediments have shorter roots and a higher leaf length:root length than plants growing in organic poor sediments. As a result, the anchoring capacity of *Zostera marina* growing in organic rich sediments may be compromised, especially considering the long leaves and high aboveground biomass that develops in these organic rich sediments. Anchoring was not a major issue in the mesocosm because there were no waves or strong currents. However, plants growing *in situ*, especially those growing adjacent to retreating marshes where wave energy is high, need to be well anchored in the sediment to counteract the drag exerted on the leaves (Gaylord et al. 1994, Peralta et al. 2000). The abundance of organic matter in old marsh peat adjacent to the retreating shoreline at Mill's Island may allow seagrass roots to stay near the surface and may allow the plants to put all their energy into aboveground production. This, in turn, may lead to a large amount of drag exerted on the plants. Therefore, in nature, the combination of retreating marsh shorelines with organic rich sediments and decreased anchoring capacity via plant morphology may lead to the absence of plants growing in sediments adjacent to retreating marshes. In summary, the sediment organic content of old marsh peat per se is not limiting seagrass growth, but as marsh retreat leads to organic rich sediments as the available substrate in the subtidal, seagrasses are absent. This is apparently due to a mismatch between plant morphology and the physical environment.

Chapter 2

Old marsh peat as seagrass habitat substrate: Is the sediment geochemistry suitable for growth?

INTRODUCTION

While many studies have focused on light (Dennison 1987, Duarte 1991, Dennison et al. 1993, Livingston et al. 1998, Longstaff and Dennison 1999) and water quality (Stevenson et al. 1993, Meyercordt and Meyer-Reil 1999, Moore and Wetzel 2000, Tomasko et al. 2001) as the primary parameters affecting seagrass distribution, other less studied environmental factors such as hydrodynamics and sediment nutrient availability are also important habitat requirements that need to be considered (Koch 2001, Kemp et al. 2004).

Sediment nutrient availability in seagrass beds is an important factor in the growth and distribution of seagrasses (Short 1983, Short 1987, Murray et al. 1992). While many tropical seagrass species are nutrient limited and therefore, respond well to nutrient fertilization experiments (Short 1987, Terrados et al. 1999), in eutrophic systems, such as those found in temperate areas of the United States, sediment nitrogen fertilization has little or no effect on seagrass growth (Dennison et al. 1987, Murray et al. 1992). In contrast, phosphorus limitation can still occur in these areas, as shown by a study on *Zostera marina* in Chesapeake Bay (Murray et al. 1992). In all these field-based studies, water column nutrient concentrations were found to affect the outcome of the experiments, illustrating the problems associated with conducting fertilization experiments *in situ*. A controlled mesocosm experiment showed that nitrogen content of

the substratum (sand versus mud), in particular porewater ammonium, controls *Zostera marina* growth (Short 1987).

Porewater nutrient concentrations are closely related to the organic content of sediments because nutrient regeneration is dependent on the amount of carbon available for bacterial metabolism (Berner 1977). Organic poor sediments, such as sand, are considered to be nutrient limiting to seagrasses due to low levels of ammonium and phosphate (Holmer et al. 2001). Conversely, organic rich sediments, such as marsh peat, typically have high amounts of ammonium and phosphate (Berner 1977). Therefore, it can be inferred that seagrasses would grow better in organic rich sediments. However, in these organic rich sediments the oxygen is quickly depleted via aerobic respiration and anaerobic respiration occurs. Sulfides result from anaerobic respiration and these can be toxic to seagrasses (Pulich 1982, Carlson et al. 1994, Brueechert and Pratt 1996). While sulfide can decrease photosynthetic activity (Goodman et al. 1995) and lead to leaf mortality (Koch and Erskine 2001), it usually occurs when another environmental stressor (e.g. low light, high temperatures, respectively) is present and at sulfide levels that are higher than normally found in healthy seagrass beds (6 mM, Koch and Erskine 2001). The current study determined the response of seagrass growth parameters to hydrogen sulfide concentrations *in situ* and in a controlled experiment to test the hypothesis that old marsh peat is limiting seagrass productivity and distribution due to its relatively high porewater sulfide concentrations. Additionally, porewater nutrients were determined *in situ* and in a controlled experiment to evaluate if sand is limiting seagrass productivity and distribution due to its low porewater nutrient concentrations.

METHODS

Study site

Mill's Island in Chincoteague Bay (Figure 1) was selected based on the presence of a retreating marsh shoreline with an adjacent seagrass bed. The present study took place at the southeast portion of the island, along a beach extending southwest to northeast. The substrate in the seagrass habitat (i.e. < 1 m water depth) was dominated by old marsh peat along the northeast shoreline and seagrass beds were absent, while the substrate in the seagrass habitat was dominated by a thin sand layer over old marsh peat along the southwest shoreline and seagrass were present (Figure 2). The source of sand was an eroding dune within the marsh system (Figure 2). As the marsh ended in the form of an abrupt scarp, the distance between the erosional marsh shoreline and the shallow edge of the seagrass bed was less than 20 m. The astronomical tidal range at the site was less than 30 cm (NOAA 2005).

Field surveys

Surveys and aerial photographs showed the seagrass bed to be narrow and to follow the shoreline. In late September 2004, dialysis porewater samplers (peepers), were placed along two transects to determine porewater ammonium, phosphate and hydrogen sulfide inside and outside the seagrass bed. One transect (outer transect) started at the base of the erosional dune and ran northeast, ending beyond the edge of the seagrass bed (Figure 3). This transect length was 340 m and covered the southwest and northeast edges of the seagrass bed. The second transect (inner transect) was parallel to the outer transect but 20 m closer to shore (Figure 3). The inner transect was 320 m long, covered the entire length of the seagrass bed and ended at the edge of the marsh. The

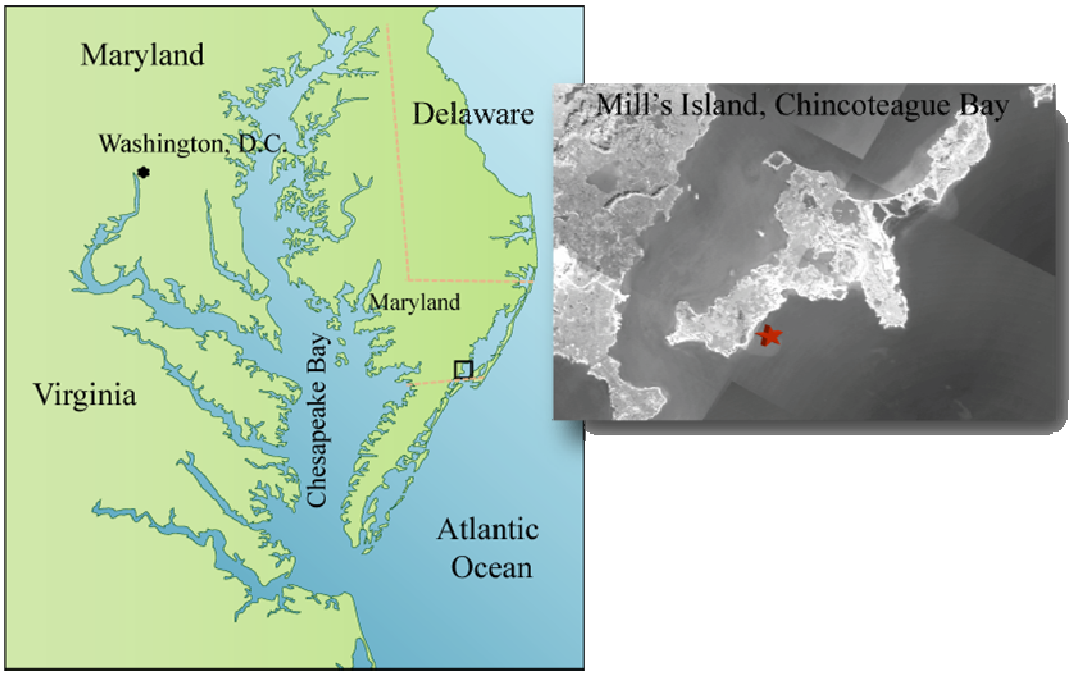
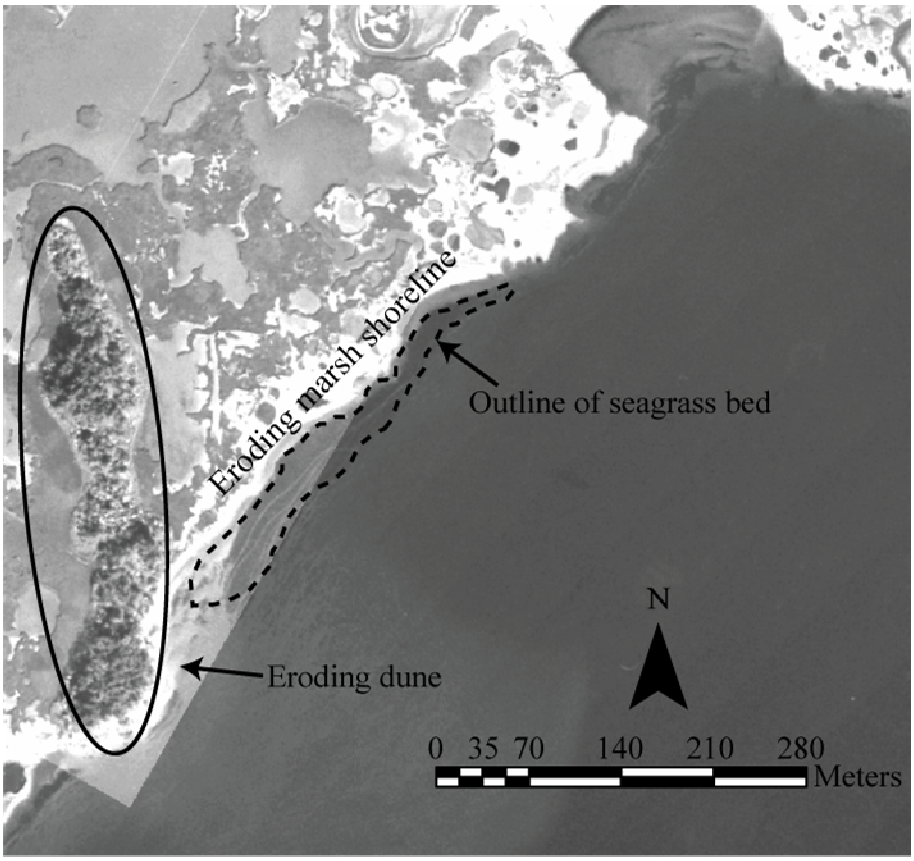


Figure 1: Location of study site ( ) at Mill's Island (38° 03' N, 75° 18' W) in Chincoteague Bay on the Eastern Shore of Maryland.

a)



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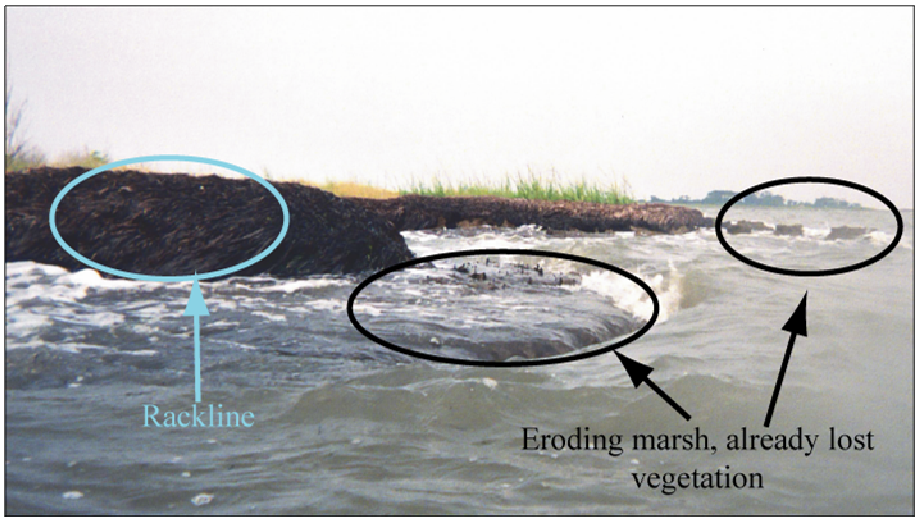


Figure 2: Location of the *Zostera marina* bed and eroding Pleistocene dune at Mill's Island. Chincoteague Bay. Maryland (a). Edge of the seagrass bed was determined by visually assessing a 2003 aerial photograph (courtesy of VIMS) for change in color between bed and bare sand. Photograph of eroding marsh shoreline at Mill's Island (b). Note the process of marsh retreat: marsh erodes from top and edge forming unvegetated platforms that continue to erode until flush with the seafloor.

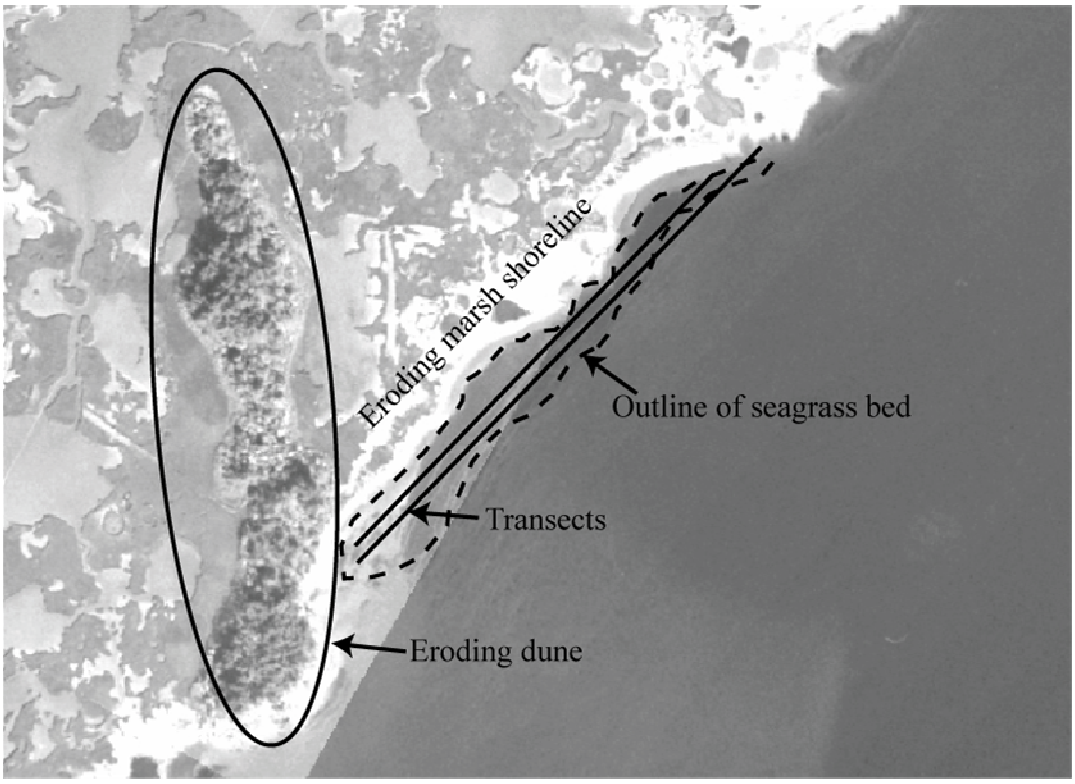


Figure 3: Transect lines for the 2004 survey of a *Zostera marina* bed at Mill's Island, Chincoteague Bay, Maryland. The 2005 survey followed the 80 cm depth contour in proximity of the 2004 inner transect.

dialysis porewater samplers measured 30 cm in length with 10 mL wells. A 0.2 micron polycarbonate membrane (Osmonics, Inc.) overlaying the wells allowed diffusion of dissolved molecules into the de-ionized water within the wells. Mesh screening (125 μm, Nitex, Sea-Gear Corporation) was placed over the membrane to prevent particulate matter from clogging the membrane. The cover plate was then screwed onto the front of the peeper to hold the membrane and screening in place. Holes corresponding to the well placement allowed the mesh screening (and therefore the wells) to be in contact with the sediment porewater. The samplers were placed at 4 pre-selected locations along the inner transect and 5 pre-selected locations along the outer transect to sample the porewater in a range of sediment types (sand, old marsh peat and sand overlaying old marsh peat) and seagrass shoot density (unvegetated and unvegetated) combinations found at Mill's Island (Table 1). The peepers were allowed to equilibrate for 14 days before they were taken out of the sediment and the water within the wells was frozen until porewater nutrient analysis could be performed (Lane 2000). At each peeper location, GPS coordinates (Garmin International, Inc. eTrex, ± 3 m), water depth (meter stick), seagrass species and shoot density (25 x 25 cm quadrat) were quantified. Sediment samples (core = 5 cm in diameter) were also taken to determine the thickness of the sand overlaying the old marsh peat and the sediment organic content of each layer. The sand and old marsh peat layers in these cores were separated based on differences in grain size and sediment color, with the sand having a higher percentage of large grain sizes than the old marsh peat. The different layers were then put in separate, labeled bags and taken to the lab for characterization of grain size and percent organic matter according to Erftemeijer and Koch (2001). At each peeper location, three samples of seagrasses were collected

Inner Transect	
Sand layer depth	Seagrass Present?
> 30 cm	Yes
> 30 cm	No
< 10 cm	Yes
< 10 cm	Yes
Outer transect	
Sand layer depth	Seagrass Present?
> 25 cm	No
> 20 cm	Yes
> 20 cm	Yes
20 cm	Yes
5 cm	No
0 cm	No

Table 1: Description of locations chosen for biomass sampling at Mill's Island in 2004.

location with a 5 cm-diameter core within 50 cm of where peepers were placed and combined into one sample per location. Prior to combining samples in one bag, all plant material was rinsed in seawater in a sieve to remove any sediment attached to the roots and rhizomes. Samples were refrigerated (6˚ C) until leaf and root length were measured (within 4 wks) via direct measurement using a ruler. Once length measurements were complete, samples were placed in a drying oven (50˚ C), dried to constant weight and weighed to determine biomass.

In June 2005, the field survey was repeated to gather more detailed data on the relationship between plant biomass, leaf and root length and sediment porewater chemistry. While the previous year's data showed a possible relationship between plant growth and sediment porewater ammonium, orthophosphate and hydrogen sulfide, there were not enough samples to make a definitive statement about whether hydrogen sulfide in sediments adjacent to retreating marshes is limiting seagrass growth. However, instead of two straight transects through the seagrass bed, fifteen points along a transect at the 80 cm depth contour were sampled, thereby eliminating depth as a co-variable. Seagrass, sediment and porewater samples were collected and processed the same way as in the previous year. However, the three seagrass samples of plant cores taken at each peeper location were kept separate as subsamples rather than combining all into one sample.

In order to relate seagrass growth to porewater nutrient and hydrogen sulfide concentrations at the study site, the porewater concentrations in the top 15 cm of sediment independent of sediment type were averaged. Using the top 15 cm ensures that the characteristics of the entire area where belowground biomass could occur (i.e.

rhizosphere of *Zostera marina* at this site) were represented in the data. This supposition is based on the maximum root lengths measured in 2004 and 2005 (9.6 ± 1.2 cm).

Sediment organic content experiment

An outdoor mesocosm (3.07 m long x 0.66 m wide x 0.60 m high) with extensive aeration for carbon dioxide supply and water movement was used to determine the response of *Zostera marina* to different sediment types (Figure 4). Use of a single mesocosm containing all organic content treatments ensured that sediment nutrients were the only variable as all plants, independent of the sediment they colonized, were exposed to the same water column nutrient concentrations. In order to obtain different sediment organic contents, different types of sediments were mixed (Table 2). The degree of compaction of the experimental sediment was lessened as the old marsh peat, which is usually hard and compacted *in situ*, was broken up before mixing with the sand. However, the 4.4% organic treatment (old marsh peat) became an unconsolidated liquid when first mixed and therefore, it was left in its natural compacted state for the experiment. Three replicates of each treatment (0.1, 0.5, 1.2, 4.4, 5.9 and 10.3% organic content) were used, totaling 18 compartments, each 25 cm long x 19 cm wide x 10.5 cm deep (Figure 5).

First, the compartments were placed in an indoor annular flume in December 2004 to ensure equilibration of geochemical gradients in the sediments. The sediments were allowed to rest in the compartments for two months under continuous water flow (10 cm s^{-1} at sediment surface) and 20˚ C. During this period the water (filtered Choptank River water, salinity = 10 to 15) was changed weekly. Using dialysis porewater samplers (peepers) (11 cm long, 10 mL wells), porewater in each compartment

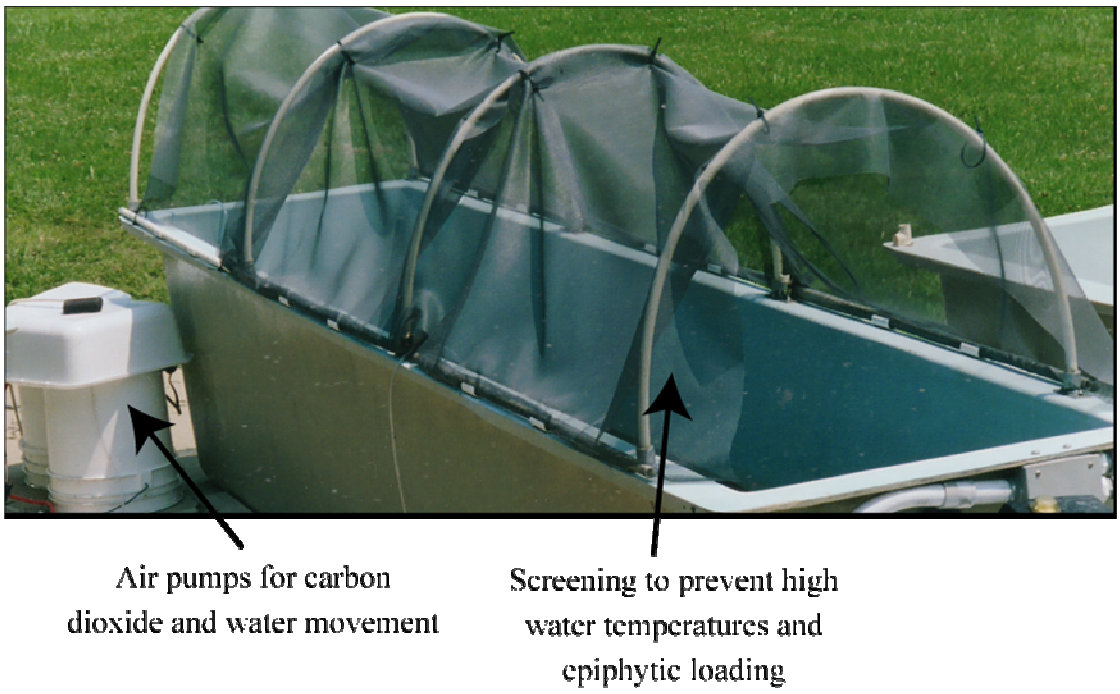


Figure 4: Outdoor mesocosm used for sediment organic content experiment. Screening helped to keep water temperatures and epiphytic loading low. Aerators (under buckets) provided carbon dioxide and water movement.

Treatment (% organic content)	Sediment Source 1	Sediment Source 2
0.1 ± 0.0	Beach dune sand[a]	—
0.5 ± 0.0	Marsh dune sand[b]	Old marsh peat[c]
1.2 ± 0.0	Marsh dune sand[b]	Old marsh peat[c]
4.4 ± 0.2	Old marsh peat[c]	—
5.9 ± 0.0	Old marsh peat[c]	Marsh sediment[d]
10.3*	Marsh sediment[d]	—

[a] Beach dune sand obtained from Assateague State Park
[b] Marsh dune sand obtained from Mill's Island, Chincoteague Bay, Maryland.
[c] Old marsh peat obtained from subtidal area adjacent to Mill's Island, Chincoteague Bay, Maryland.
[d] Marsh sediment obtained from Horn Point Marsh, Cambridge, Maryland. Sediment was a mixture of decomposed marsh vegetation and soil.
* Only one sample analyzed for organic content.

Table 2: Sources of sediment used to obtain a range of sediment organic content treatments for the mesocosm experiment.

was sampled for the analysis of ammonium, orthophosphate concentrations and hydrogen sulfide (Lane 2000). Forty-eight hours before the peepers were added, the salinity was increased to 28, which is more realistic for salinities experienced by the seagrass species tested. To minimize the artifact introduced by porewater advection along the edges of the compartments, the peepers were placed such that the wells were directly in the center of each compartment. Peepers were placed in the flume on two occasions: (1) from March 3 to 18 to evaluate porewater ammonium, orthophosphate and hydrogen sulfide concentrations before the experiment began and (2) from June 9 to 16 to determine the porewater nutrients while the plants were growing. After the peepers had been removed from the sediment on March 18th, the holes remaining were filled with the same treatment sediment. The sediment was allowed to naturally compact and settle and the geochemical processes of the sediment to equilibrate for five weeks before the experiment began.

The compartments were moved to the outdoor mesocosm in April 2005 for the start of the experiment. The mesocosm was covered with two layers of neutral density screening to prevent the water from excessive heating and to minimize epiphytic growth. Two air pumps (Optima, #807) provided carbon dioxide and water movement. Choptank River water was combined with Crystal Sea Marinemix (Marine Enterprise International) to raise the salinity to equal that of the collection site (salinity = 28) and a 50% water change occurred weekly. *Zostera marina* seedlings (single shoots) from Chincoteague Bay were planted in the compartments (4 plants compartment^{-1}) in April 2005 and were allowed to grow for eight weeks. At the end of the experiment, plant biomass and length (leaf and root) were determined the same way as for field samples.

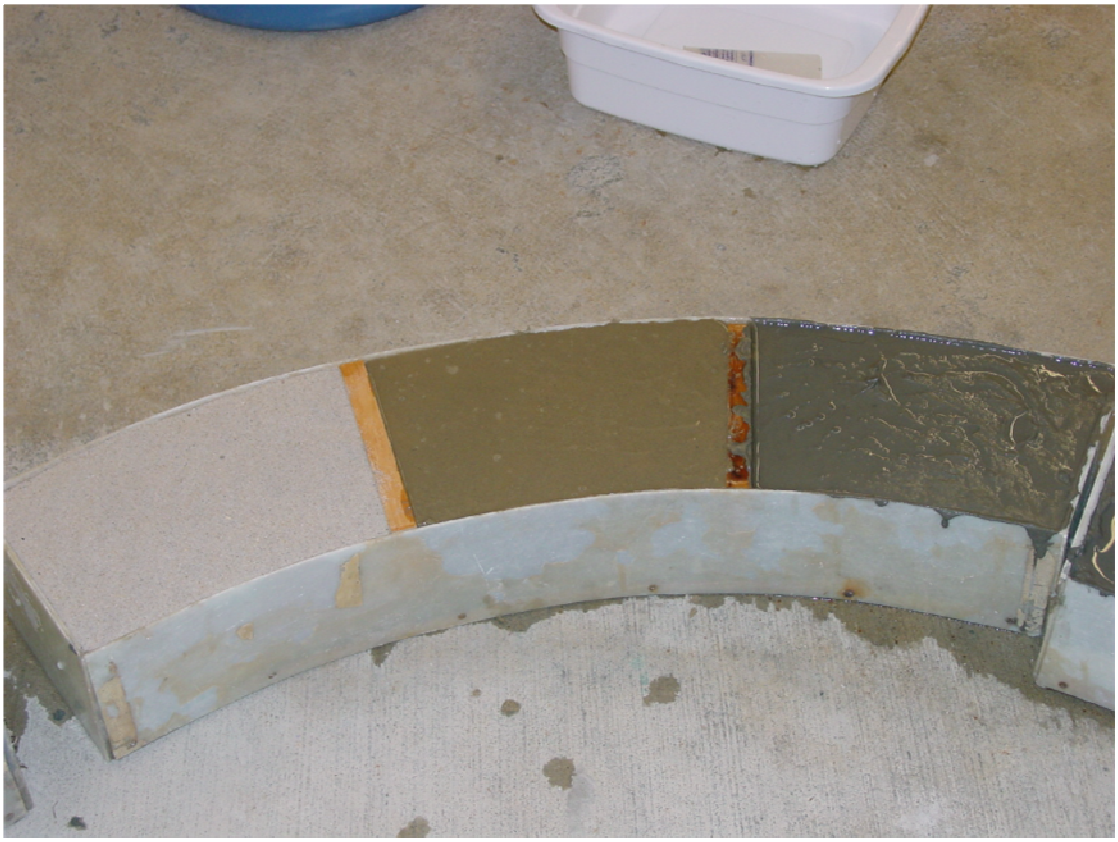


Figure 5: Compartments (25 cm long x 19 cm wide x 10.5 cm deep) with different sediments used for the organic content experiment an in outdoor mesocosm. Left to right: 0.1%. 1.2% and 4.4% organic content.

RESULTS

Field surveys

The sand in the subtidal area adjacent to Mill's Island had an organic content of 1.0 ± 0.17 % and was dominated by fine sand, while the old marsh peat had a sediment organic content of 4.8 ± 0.32 % and was dominated by silt/clay (see Chapter 1). For both 2004 and 2005, porewater profiles were divided into sites where the majority of porewater samples were within the sand layer and sites where the majority of porewater samples were within the old marsh peat layers. Therefore, some profiles considered under the old marsh peat category had a thin layer of sand overlaying the old marsh peat, but the actual sample points were mainly within the old marsh peat.

Porewater ammonium concentrations in both sediment types in 2004 were found to be in the 0.98 – 400 μM range. Ammonium concentrations were depleted in the top 15 cm of the vegetated organic poor sand (compared to an unvegetated site, Figure 6), an area where the majority of roots were also concentrated (Figure 6 inset). In old marsh peat, ammonium concentrations were similar to those found in unvegetated organic poor sand and were similar in both a vegetated and an unvegetated location (Figure 7). Roots did not seem to have an effect on the amount of porewater ammonium (Figure 7 inset). Seagrass shoot density, aboveground and belowground biomass and leaf and root length did not show a trend with average porewater ammonium concentrations.

Porewater phosphate concentrations followed the same pattern as ammonium at Mill's Island in 2004, with vegetated sand having low phosphate levels and unvegetated sand having similar concentrations to old marsh peat (Figure 8). Root length corresponded to the depth at which phosphate levels were depleted (Figure 8 inset). Both

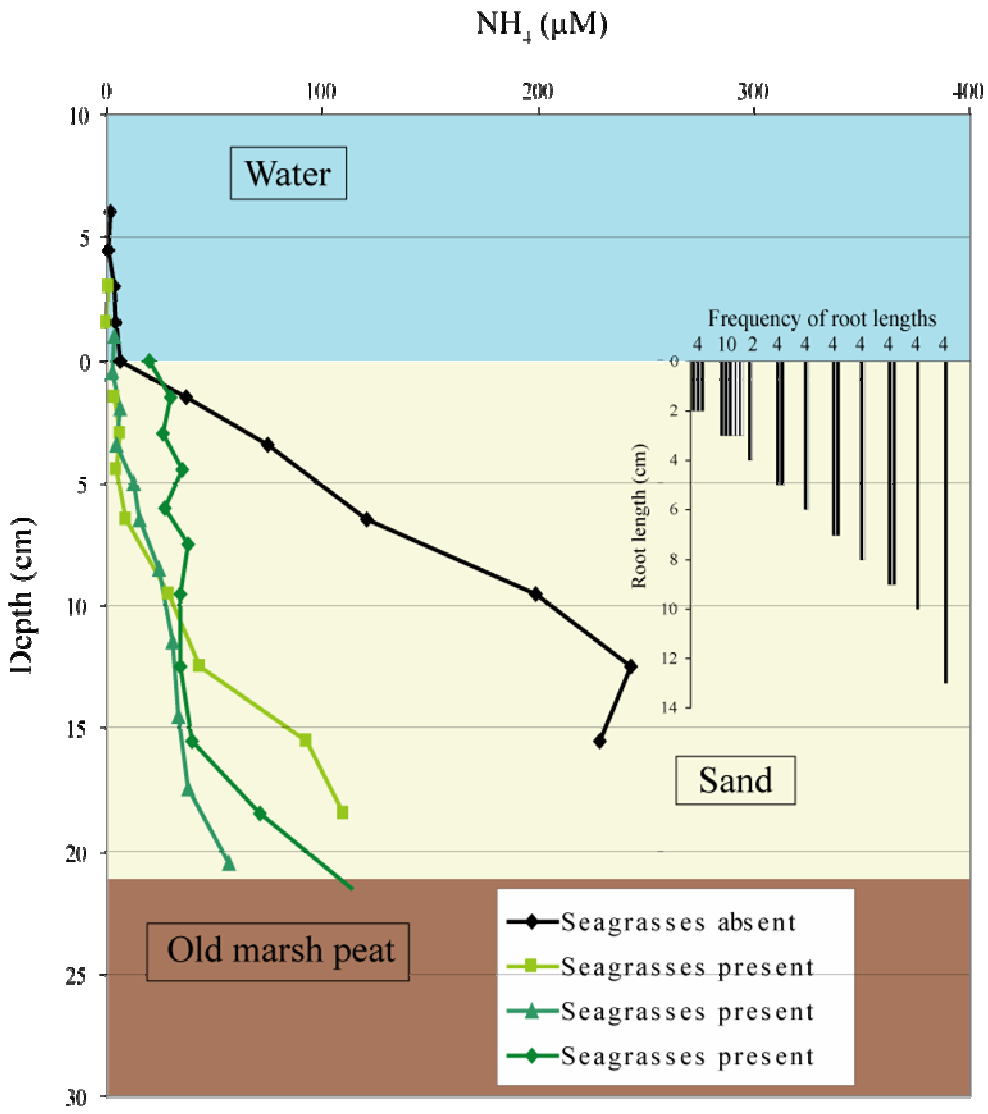


Figure 6: Porewater ammonium profiles at vegetated and unvegetated sites at Mill's Island where organic poor sand overlaying old marsh peat averaged 22 cm in depth in 2004. The rhizosphere is represented in the inset. Each vertical line represents a root. Note that the rhizosphere corresponds with the area where ammonium was depleted.

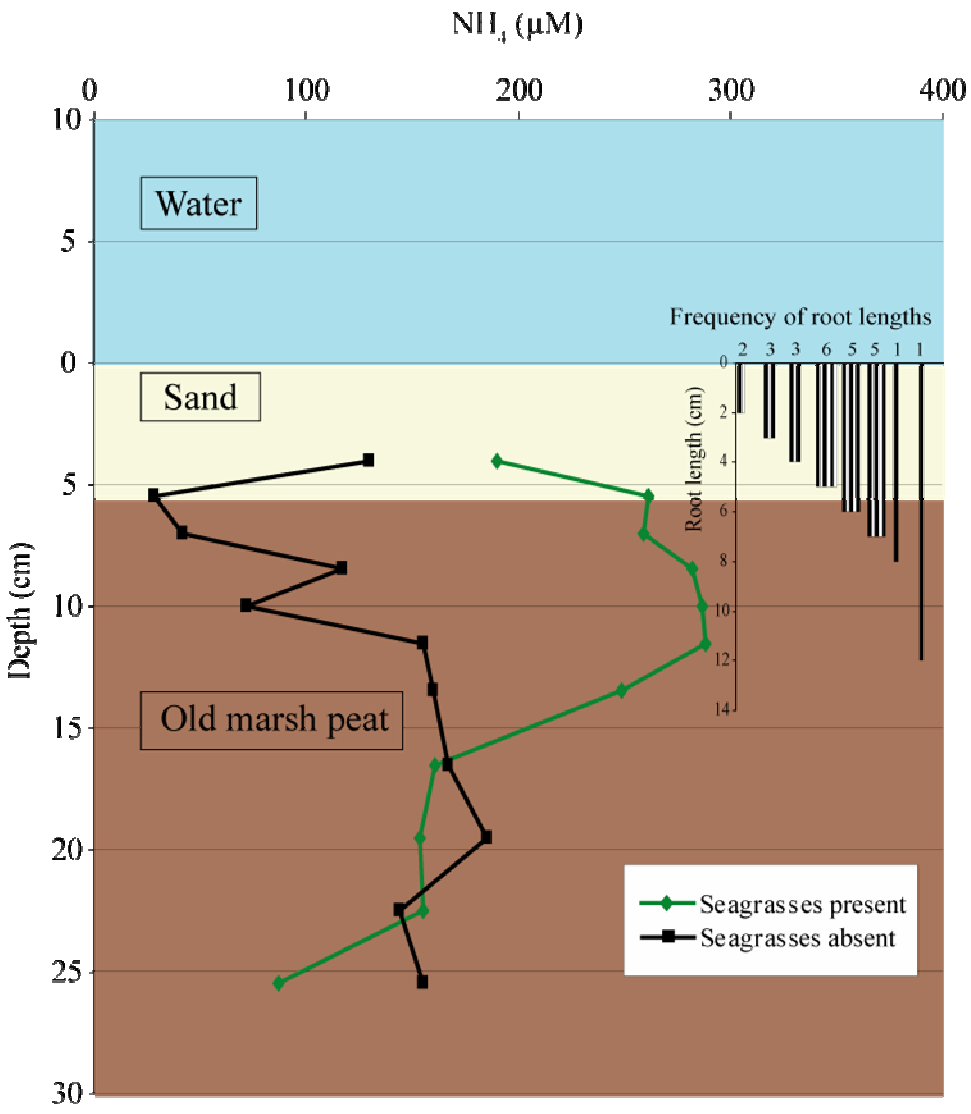


Figure 7: Porewater ammonium profiles at vegetated and unvegetated sites where only a thin layer of sand (~ 5 cm) overlays old marsh peat at Mill's Island in 2004. The rhizosphere is represented in the inset. Each vertical line represents a root.

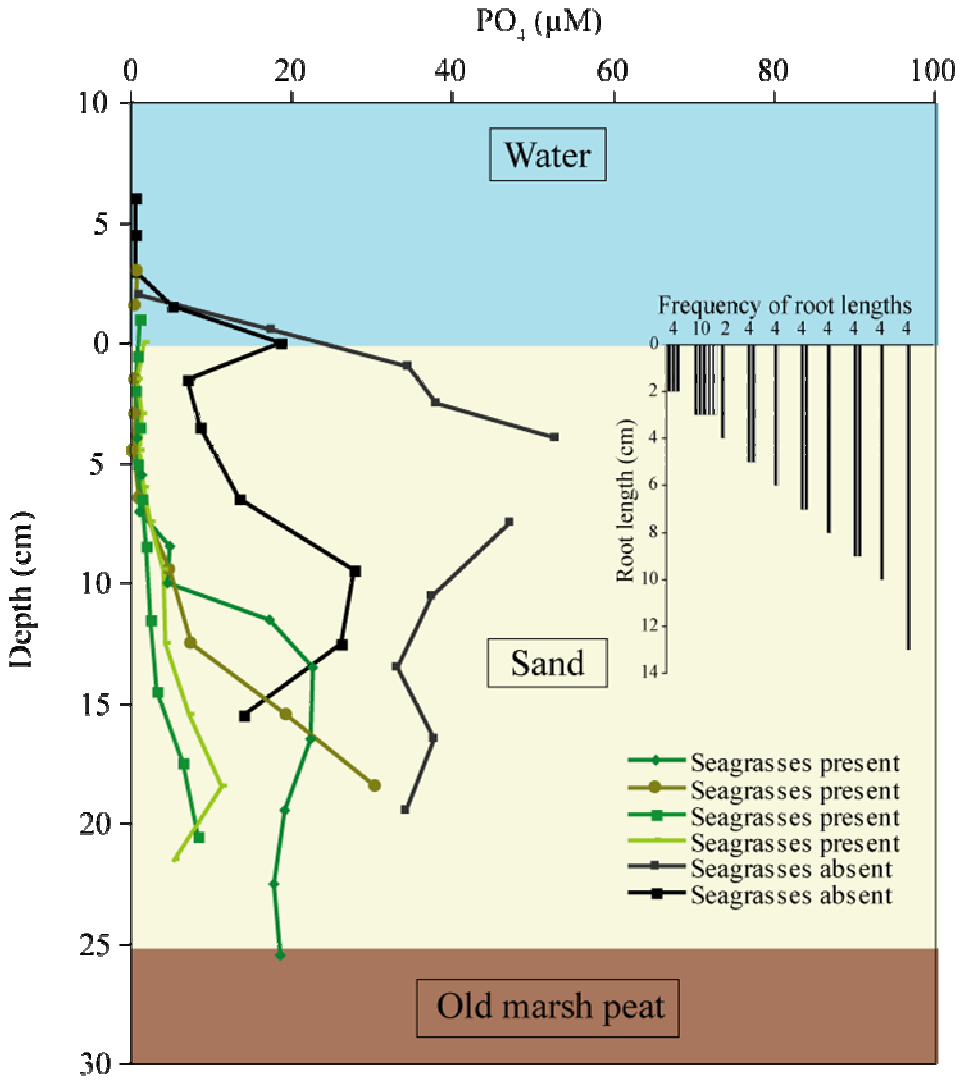


Figure 8: Porewater phosphate profiles at vegetated and unvegetated sites at Mill's Island where organic poor sand overlaying old marsh peat averaged 22 cm in depth in 2004. The rhizosphere is represented in the inset. Each vertical line represents a root.

vegetated and unvegetated old marsh peat had similar concentrations of porewater phosphate (Figure 9). Seagrass shoot density, aboveground and belowground biomass and leaf and root length did not show a trend with average porewater phosphate concentrations in the rhizosphere.

Porewater hydrogen sulfide levels were below 1.0 mM in the top 15 cm and below 0.50 mM in the top 10 cm at Mill's Island in 2004, regardless of vegetation or sediment type (Figure 10). These areas (15 and 10 cm) correspond to the maximum root length (rhizosphere) and where most of the root biomass was located, respectively. However, roots can penetrate 30 cm or more in Chincoteague (Dennison and Stevenson, pers. com.) and sulfide concentrations did reach 1.8 mM in one core. In two of the three vegetated samples where the sand layer was about 5 cm deep, sulfide concentrations doubled below 15 cm depth (Figure 10). Aboveground (r^2= 0.41) and belowground biomass (r^2= 0.58) increased with increasing average hydrogen sulfide concentrations found in the rhizosphere (Figure 11). There was no trend between seagrass shoot density, leaf and root length and hydrogen sulfide concentrations.

Porewater nutrient concentrations at Mill's Island in 2005 showed a less clear pattern than in 2004. Similar to the 2004 data, results for samples taken at Mill's Island in 2005 were divided into two groups: (1) sites where there were porewater samples in the sand layer and (2) sites where all porewater samples were within the old marsh peat layer (even if some sand was overlaying the old marsh peat). These groupings were based on sand overlaying peat and old marsh peat alone with one or two exceptions. Neither presence/absence of seagrasses nor root length showed a trend with ammonium concentrations at sand locations (i.e. sand layer > 9.3 cm) in 2005 (Figure 12). Unlike

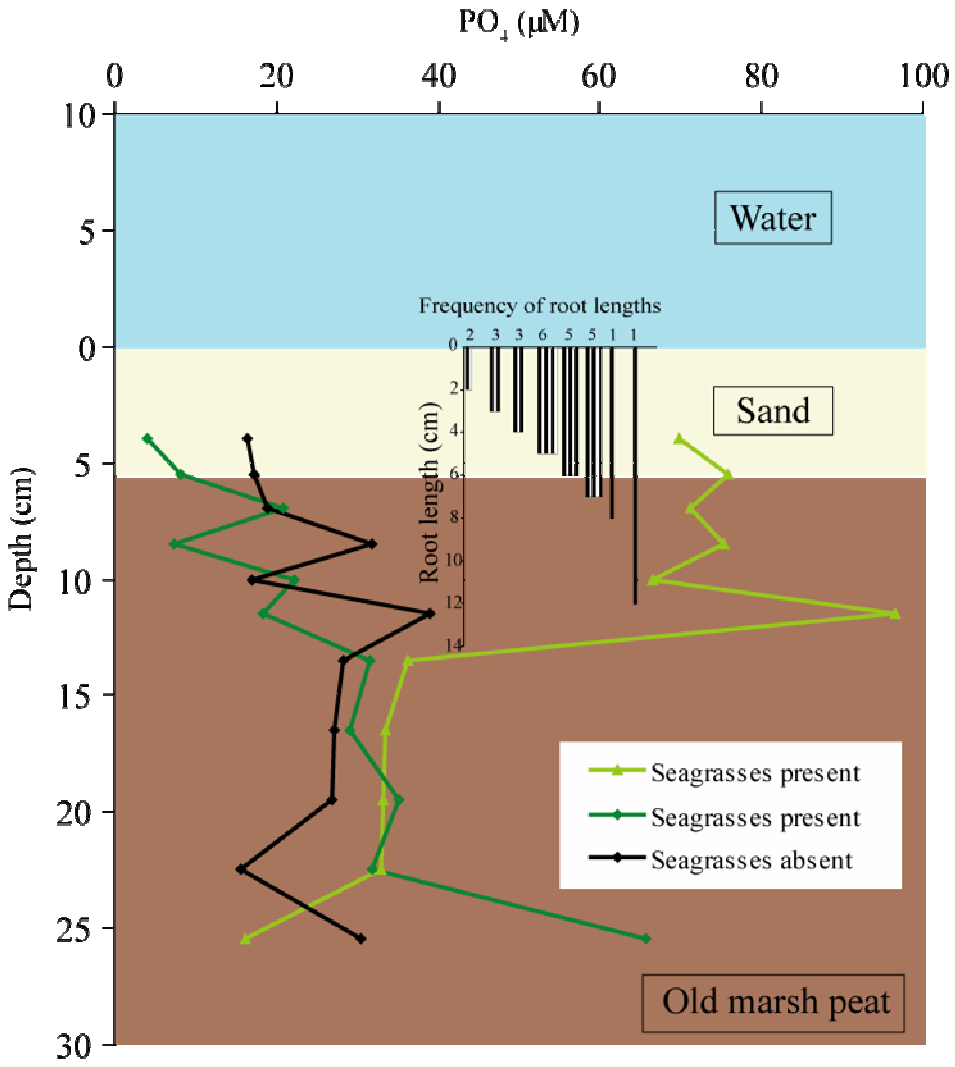


Figure 9: Porewater phosphate profiles at vegetated and unvegetated sites where only a thin layer of sand (~ 5 cm) overlays old marsh peat at Mill's Island in 2004. Phosphate in vegetated sites (green lines) equaled or exceeded phosphate in an unvegetated site (black line). The rhizosphere is represented in the inset. Each vertical line represents a root.

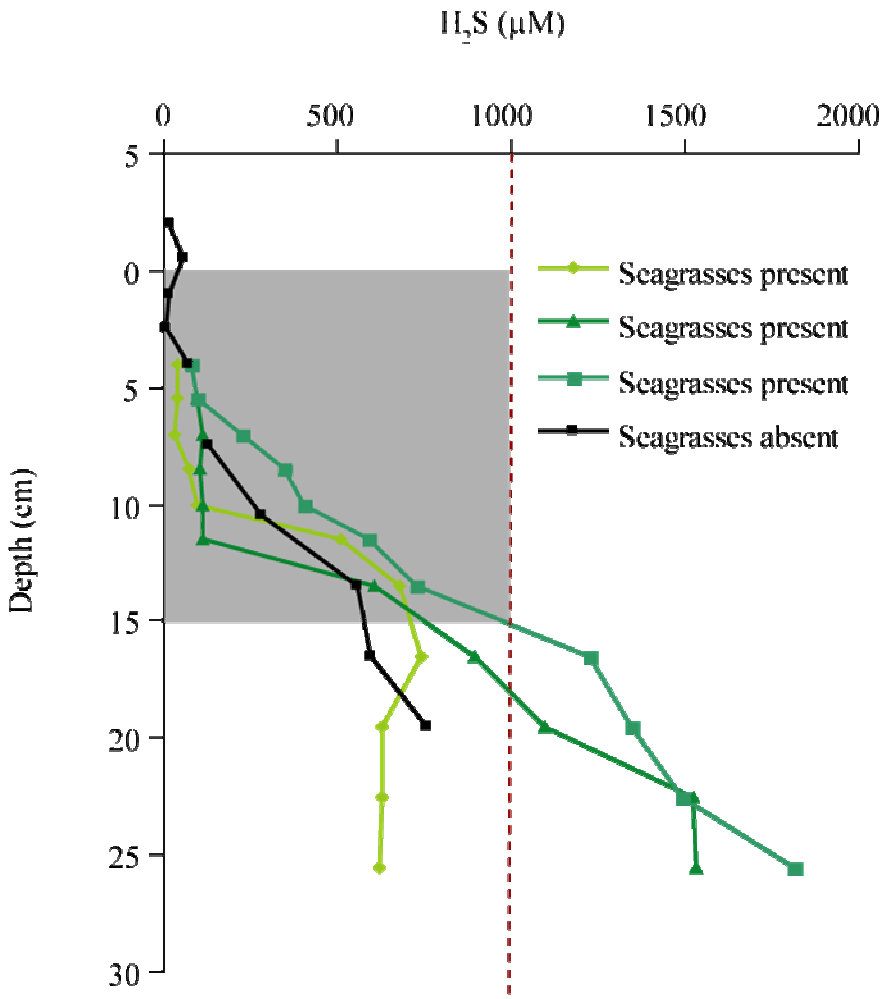


Figure 10: Porewater profiles of hydrogen sulfide at vegetated and unvegetated in a variety of sediments (sand overlaying old marsh peat) at Mill's Island in 2004. The red vertical line represents the hydrogen sulfide concentration at which seagrasses start to decline (Kemp et al. 2004). The gray box indicates the rhizosphere.

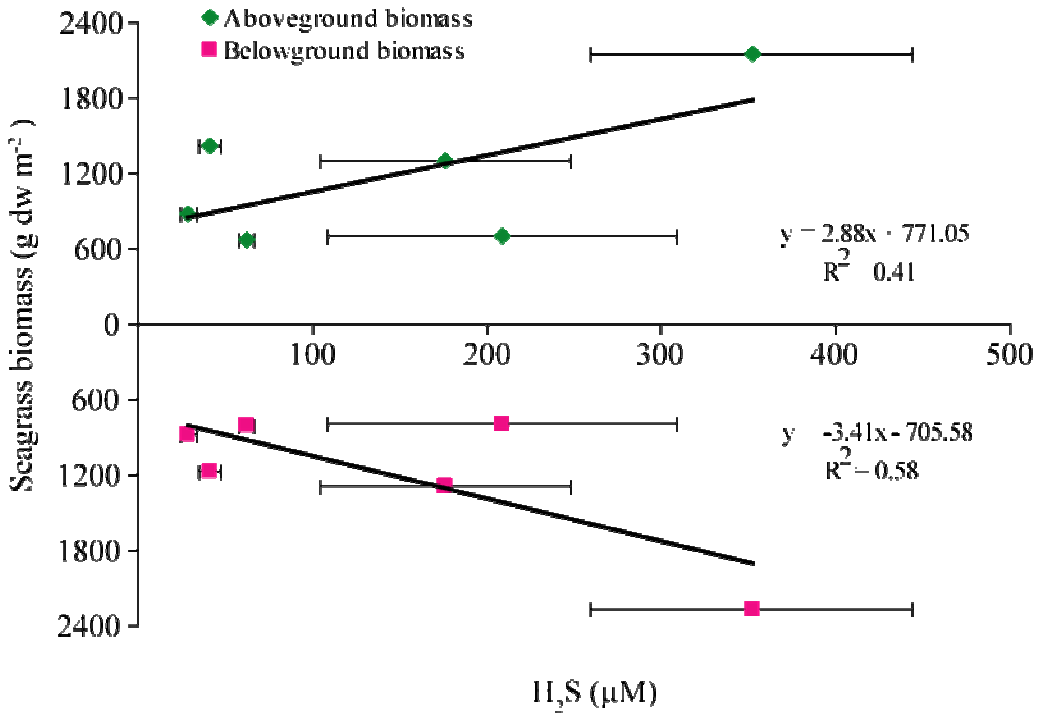


Figure 11: Aboveground and belowground biomass of *Zostera marina* at Mill's Island in 2004 as a function of hydrogen sulfide concentrations in the top 15 cm of sediment (depth of rhizosphere), independent of sediment type. Horizontal lines represent SE.

2004, porewater ammonium did not show a pattern with respect to sediment type (i.e. sand and old marsh peat), but as in 2004, ammonium concentrations in old marsh peat were similar to those in the sand. Most concentrations at vegetated and unvegetated sites increased at or below 10 cm depth (depth where root biomass decreases) and were at or above 200 μM at this depth (Figures 12 and 13). Seagrass shoot density did not show a trend with porewater ammonium concentrations (Figure 14). Average aboveground and belowground biomass did not show a trend with porewater ammonium concentrations, although there were several sampling points where biomass tended to decrease when ammonium concentrations increased above 200 μM (Figures 15). Leaf and root length did not show a trend with porewater ammonium concentrations (Figure 16).

Porewater phosphate profiles were less variable between sand and old marsh peat than ammonium profiles at Mill's Island in 2005. In sandy sediments, phosphate concentrations were below 25 μM until a depth of 10 cm. Below 10 cm, concentrations either increased to a maximum of 40 μM or decreased slightly from their maximum value (Figure 17). Phosphate concentrations were higher in old marsh peat than in the sand with the exception of two sites. These sites were unvegetated, with no sand overlaying the old marsh peat and had low phosphate concentrations (Figure 18). Neither presence/absence of seagrasses nor root length showed a trend with average phosphate concentrations in the rhizosphere. Seagrass shoot density did not show a trend with average porewater phosphate concentrations (Figure 19). Although there was a slight increase in average aboveground biomass with increasing average porewater phosphate, overall there was no trend between average aboveground biomass and average porewater phosphate (Figure 20). There was no trend between average belowground biomass,

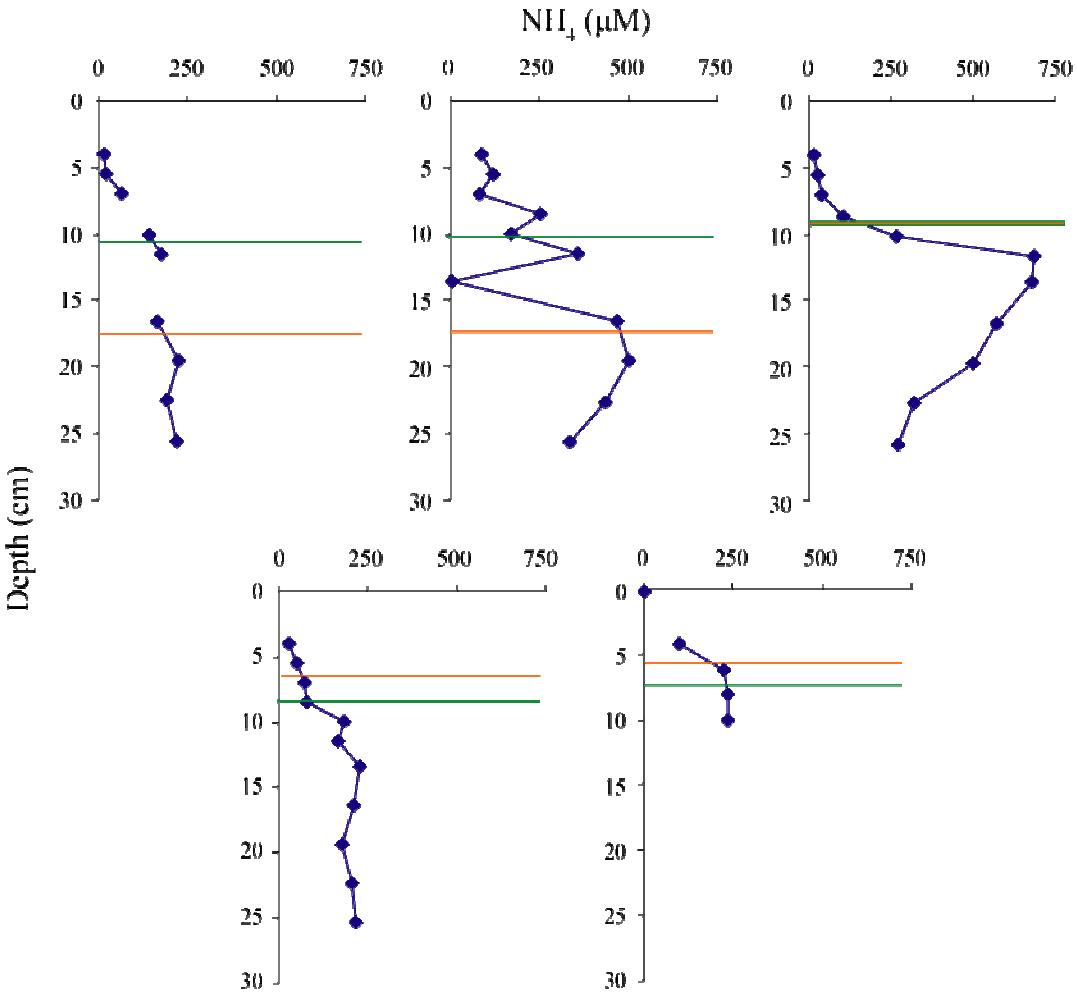


Figure 12: Porewater ammonium profiles of locations with sand (> 5 cm) overlaying old marsh peat at Mill's Island in 2005. Green lines represent maximum root length and orange lines represent sand layer depth at each location.

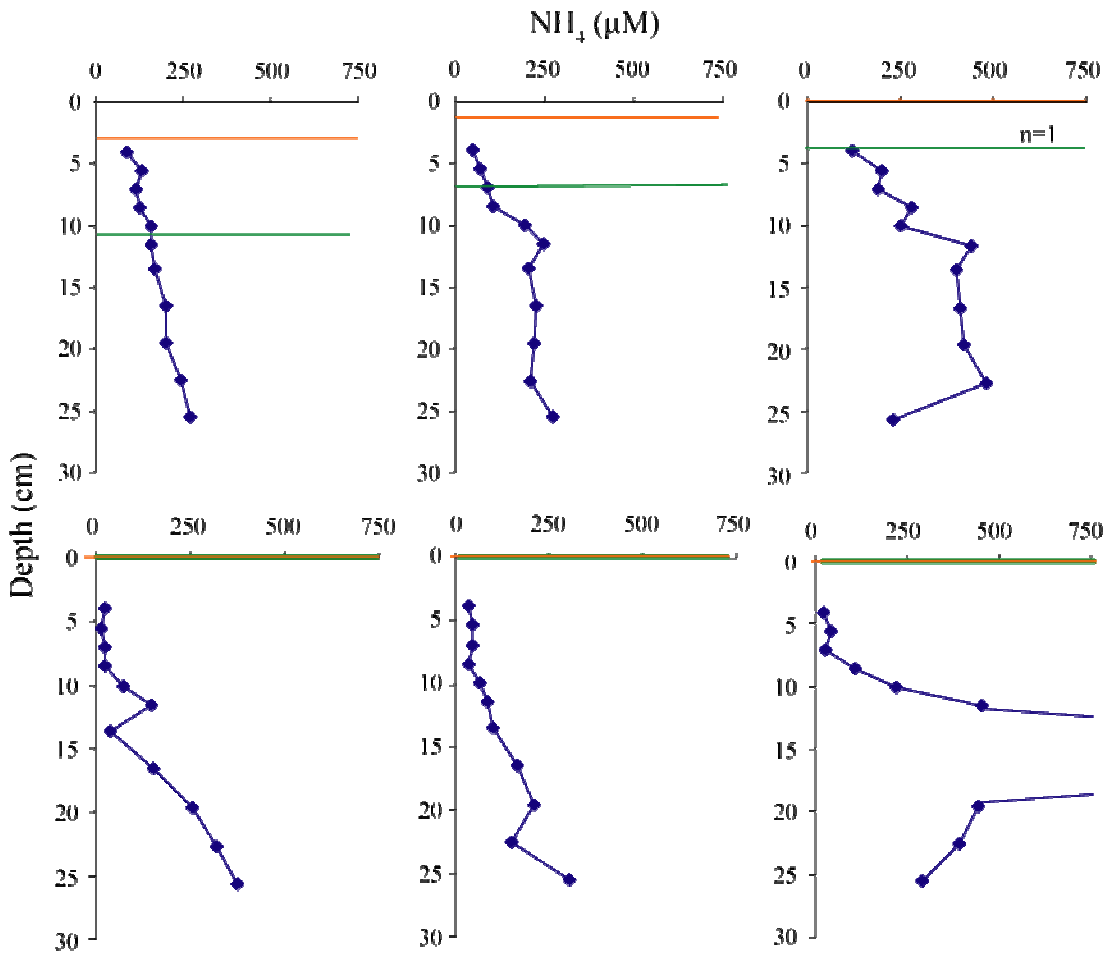


Figure 13: Porewater ammonium profiles of locations with old marsh peat (i.e. sand layer < 5 cm) at Mill's Island in 2005. Green lines represent maximum root depth and orange lines represent sand layer depth at each location. When orange and green lines = 0 cm. the site is unvegetated and characterized by old marsh peat only. Note that n=1 in top right graph represents a mostly unvegetated site with one clump of seagrasses.

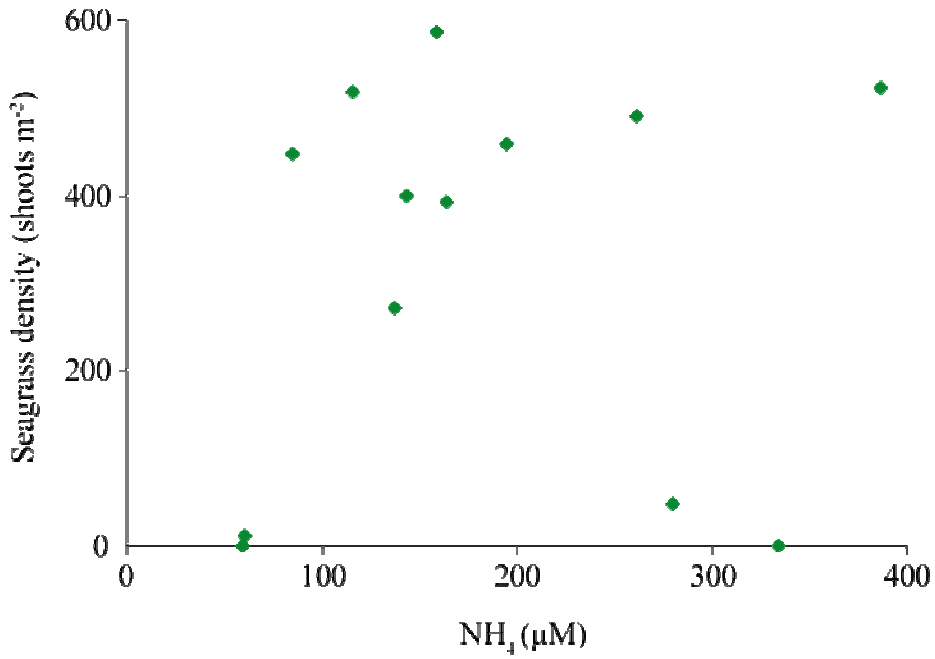


Figure 14: *Zostera marina* shoot density as a function of porewater ammonium concentrations at Mill's Island in 2005.

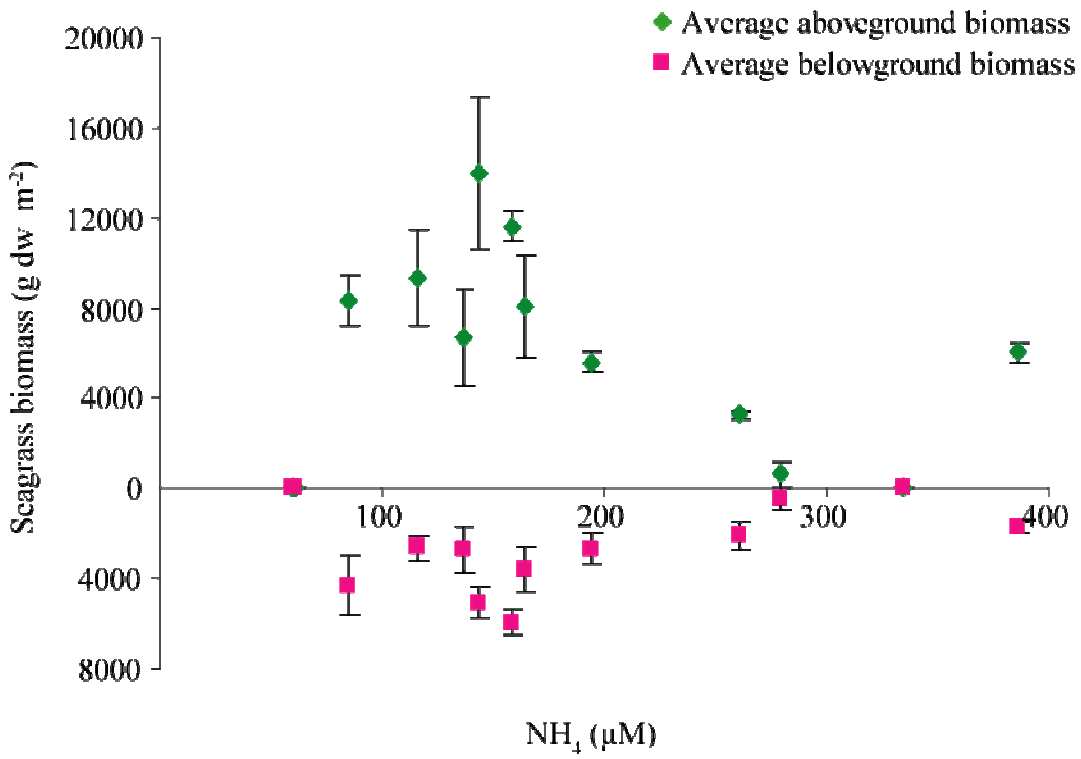


Figure 15: Average aboveground and belowground biomass of *Zostera marina* compared to porewater ammonium at Mill's Island in 2005. Note the lower biomass at concentrations > 200 µM. Vertical lines represent SE.

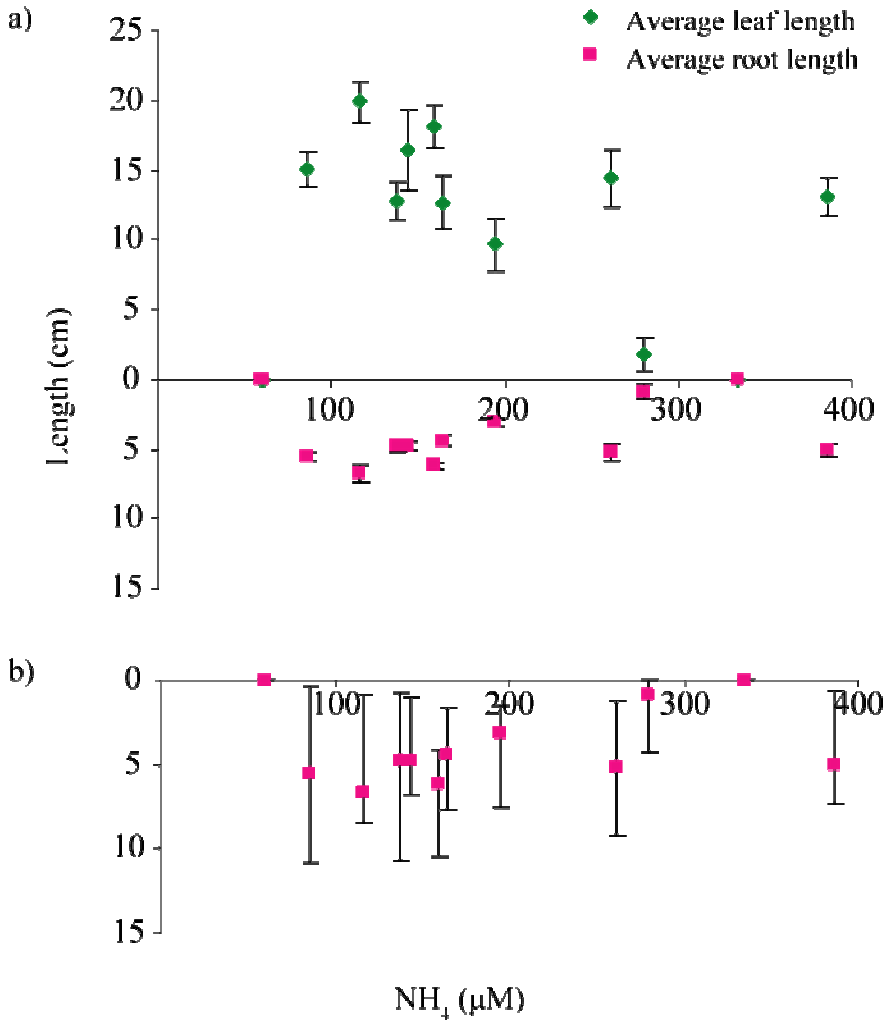


Figure 16: Average *Zostera marina* leaf and root length compared to pore-water ammonium concentrations at Mill's Island in 2005. Vertical lines in graph (a) represent SE while bars in graph (b) represent minimum and maximum root length.

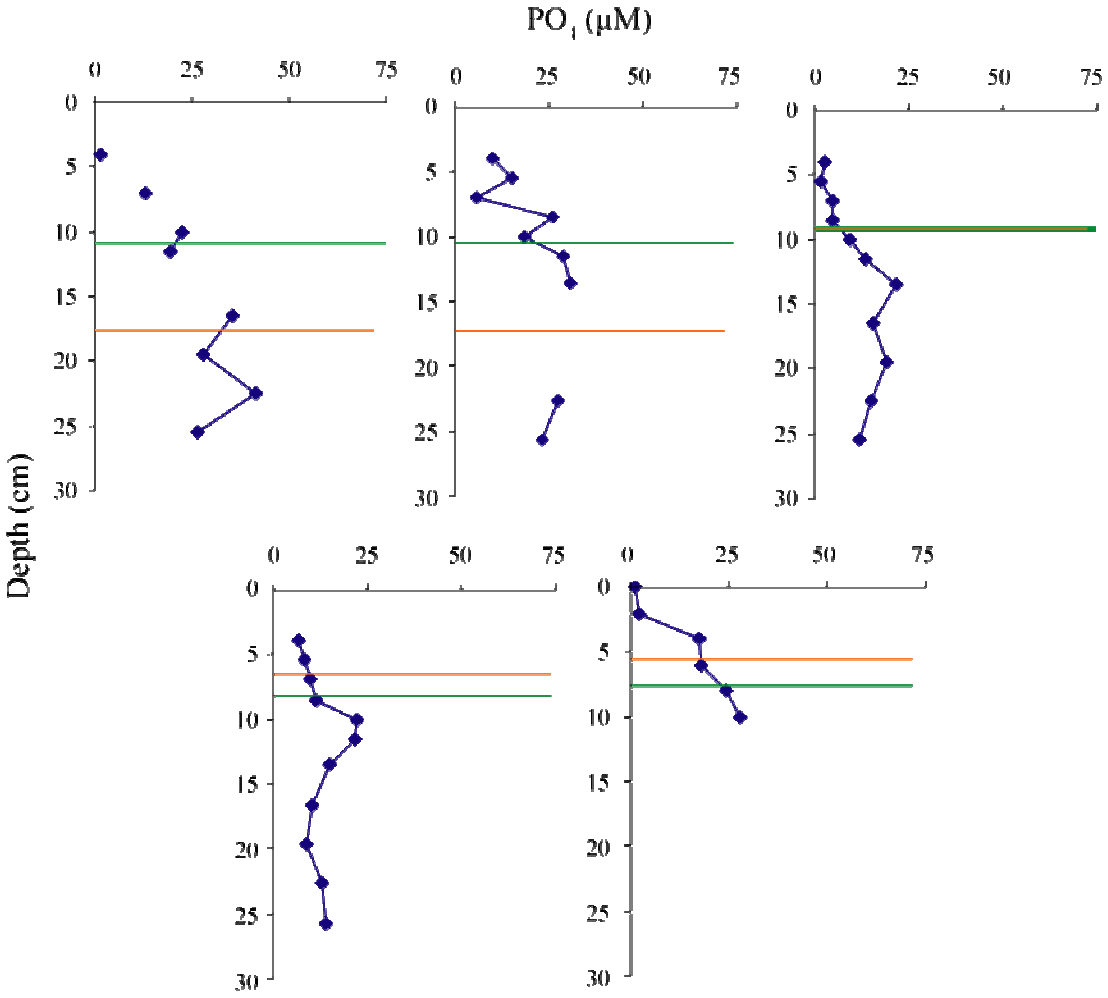


Figure 17: Porewater phosphate profiles of locations with sand (> 5 cm) overlaying old marsh peat at Mill's Island in 2005. Green lines represent maximum root length and orange lines represent sand layer depth at each location.

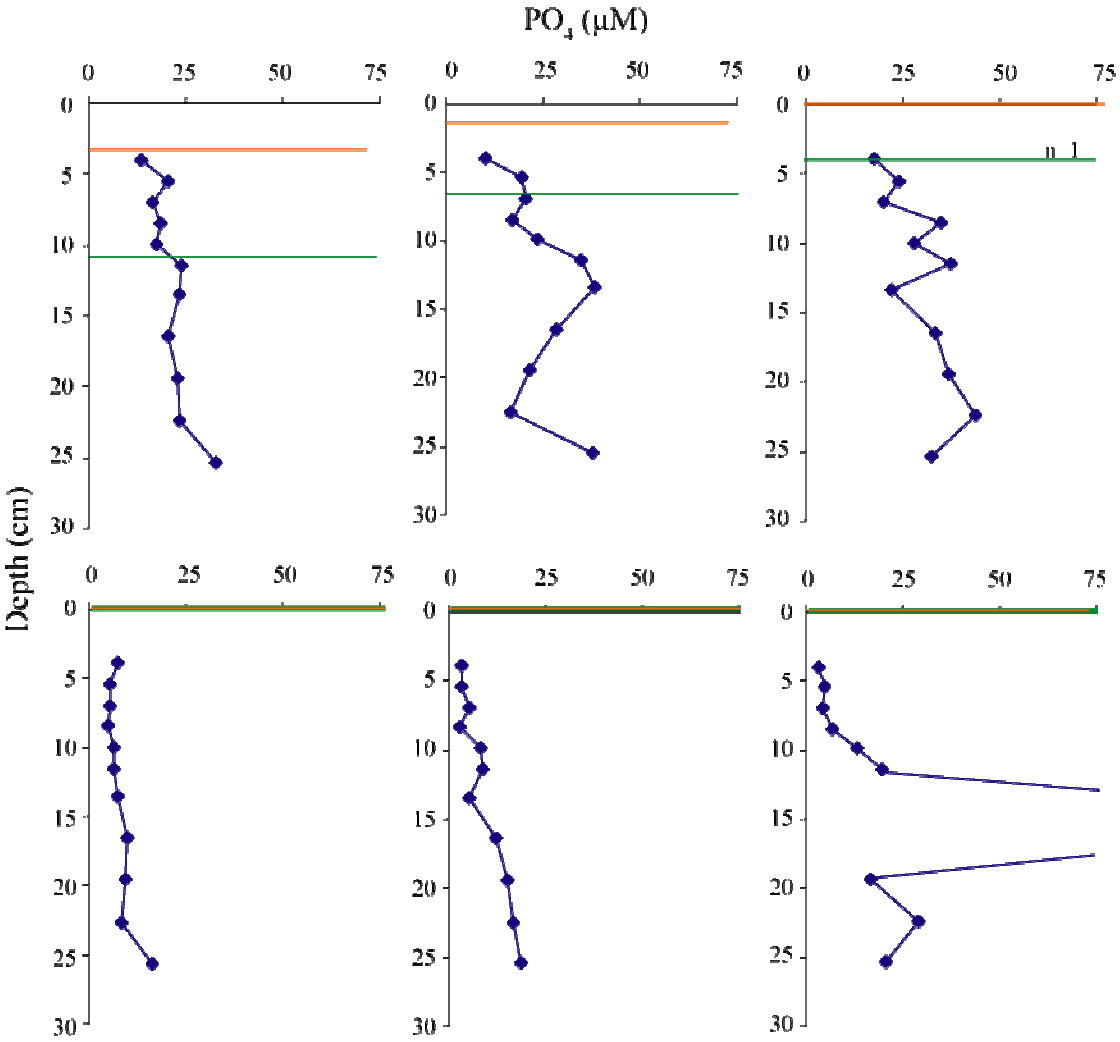


Figure 18: Porewater phosphate profiles of locations with old marsh peat (i.e. sand layer depth < 5 cm) at Mill's Island in 2005. Green lines represent maximum root length and orange lines represent sand layer depth at each location. Note that n=1 in top right graph represents a mostly unvegetated site with one clump of seagrasses.

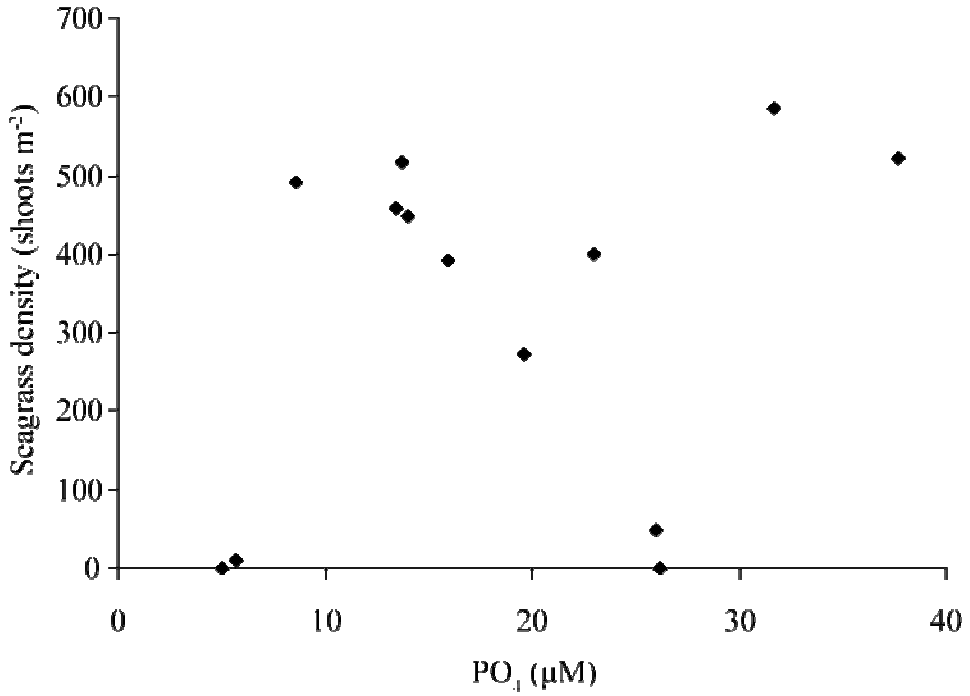


Figure 19: Shoot density of *Zostera marina* as a function of porewater phosphate concentrations at Mill's Island in 2005.

average leaf length or average root length and average porewater phosphate (Figures 20 and 21).

Porewater hydrogen sulfide concentrations were similar within sand and within old marsh peat samples at Mill's Island in June 2005. In sand and in sand overlaying old marsh peat, the maximum root length (9.3 ± 0.6 cm) was always equal or less than the depth at which sulfide concentrations reached an average of 810 ± 89.6 μM (Figure 22). Hydrogen sulfide concentrations in old marsh peat were not higher than concentrations in sand and did not reach toxic levels (1000 μM) until below the rhizosphere (i.e. depths > 15 cm, Figure 23), except for one site where hydrogen sulfide concentrations reached 1000 μM at 11.5 cm. Seagrass shoot density, average biomass and average length were variable across all average hydrogen sulfide concentrations, i.e. there was no trend (Figures 24 and 25).

Sediment organic content experiment

Porewater nutrient and hydrogen sulfide concentrations in the mesocosm changed over the course of the experiment (Figure 26). The initial nutrient and hydrogen sulfide concentrations can be interpreted as affecting seagrass growth and the final concentrations as reflecting the plants' effects on sediment nutrients. It is also possible that water column nutrients may have affected porewater nutrients of the more permeable (less organic) sediments, due to advection during the course of the experiment (Koch and Huettel 2000). Therefore, the results of seagrass growth parameters to the nutrient concentrations at the beginning of the experiment are presented.

The characteristics of the sediment in the high organic treatment (10.3%) were different than the other five treatments. The texture was a loam, rather than a sand or

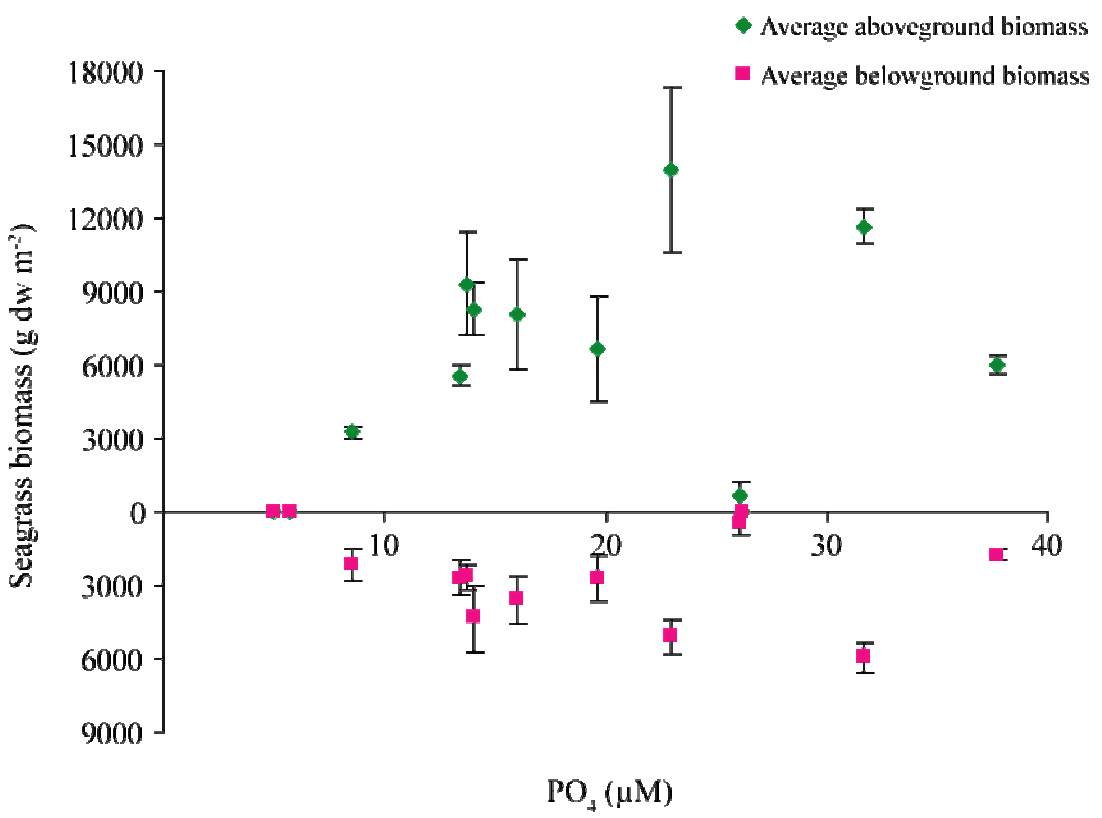


Figure 20: Average aboveground and belowground biomass of *Zostera marina* as a function of porewater phosphate concentrations at Mill's Island in 2005. Vertical lines represent SE.

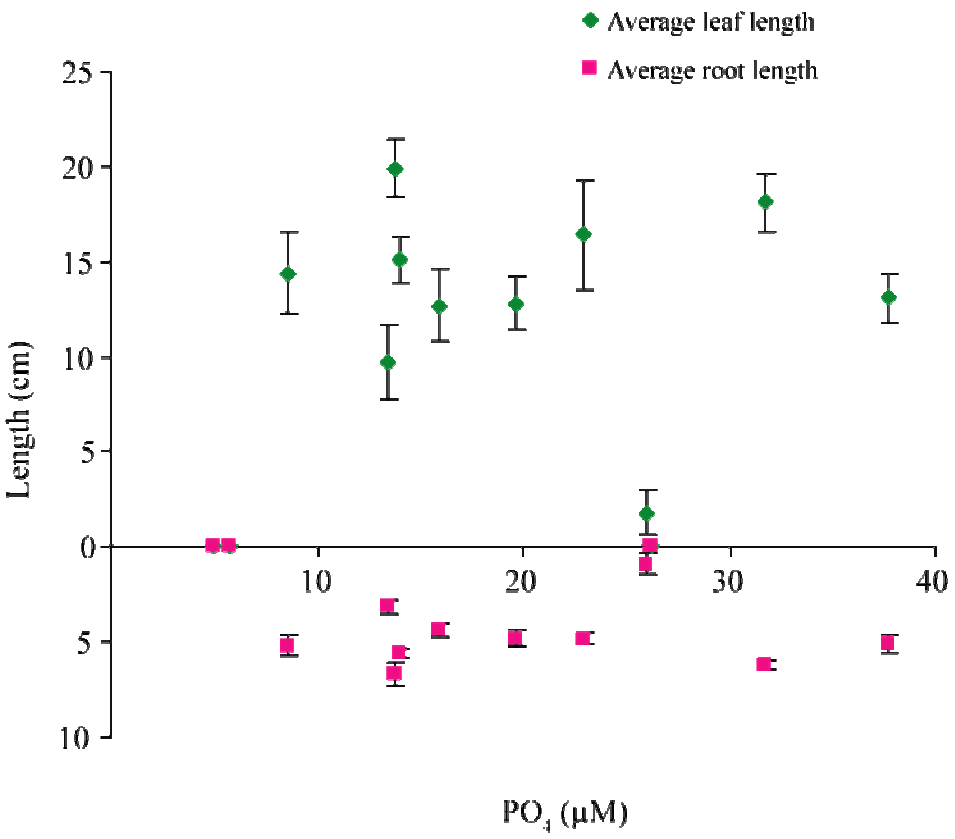


Figure 21: Average *Zostera marina* leaf and root length as a function of porewater phosphate concentrations at Mill's Island in 2005. Vertical bars represent SE.

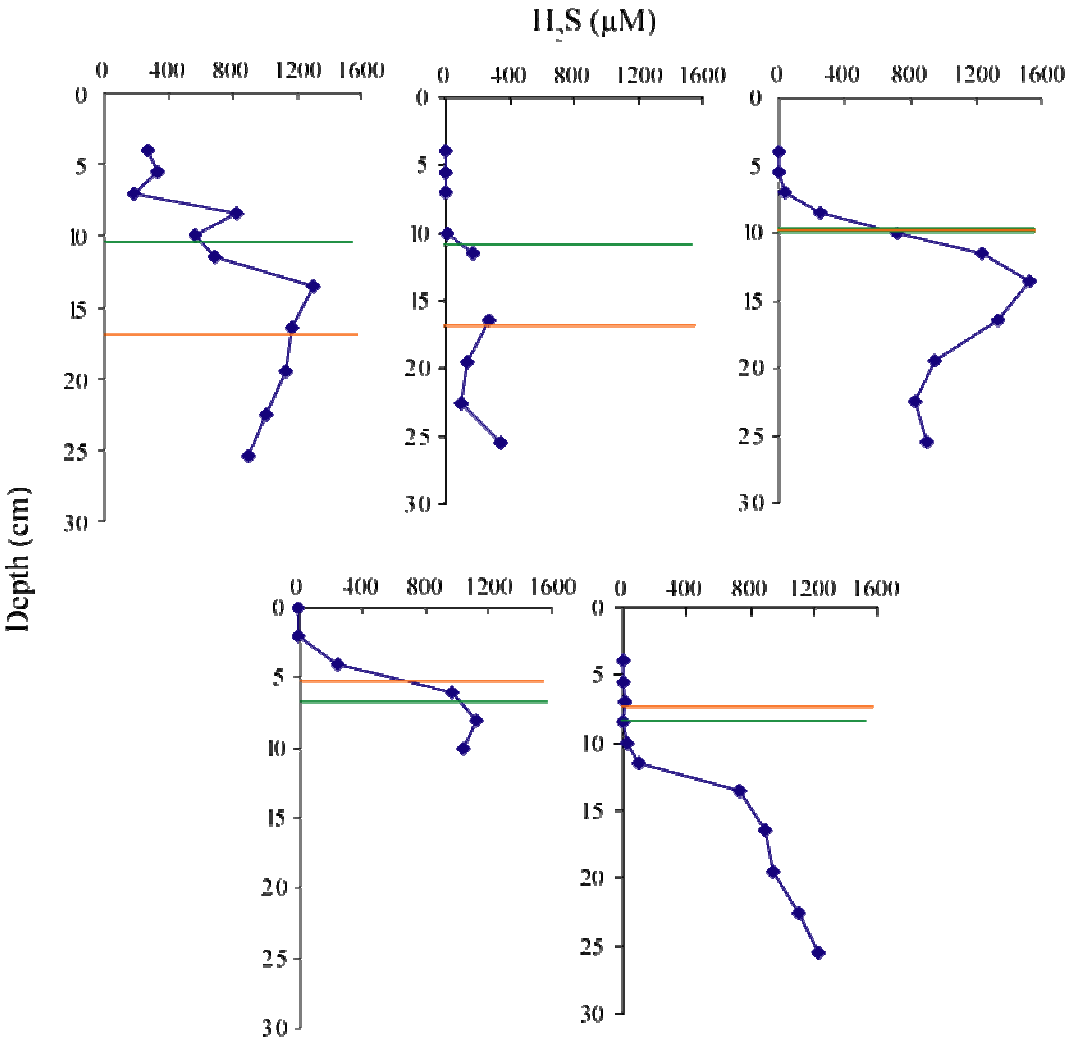


Figure 22: Hydrogen sulfide profiles of locations with sand (> 5 cm) overlaying old marsh peat at Mill's Island in June 2005. Green lines represent maximum root length and orange lines represent sand layer depth at each location. Note that maximum root length stops at the same time that hydrogen sulfide levels increase above an average of 810 ± 89.6 µM.

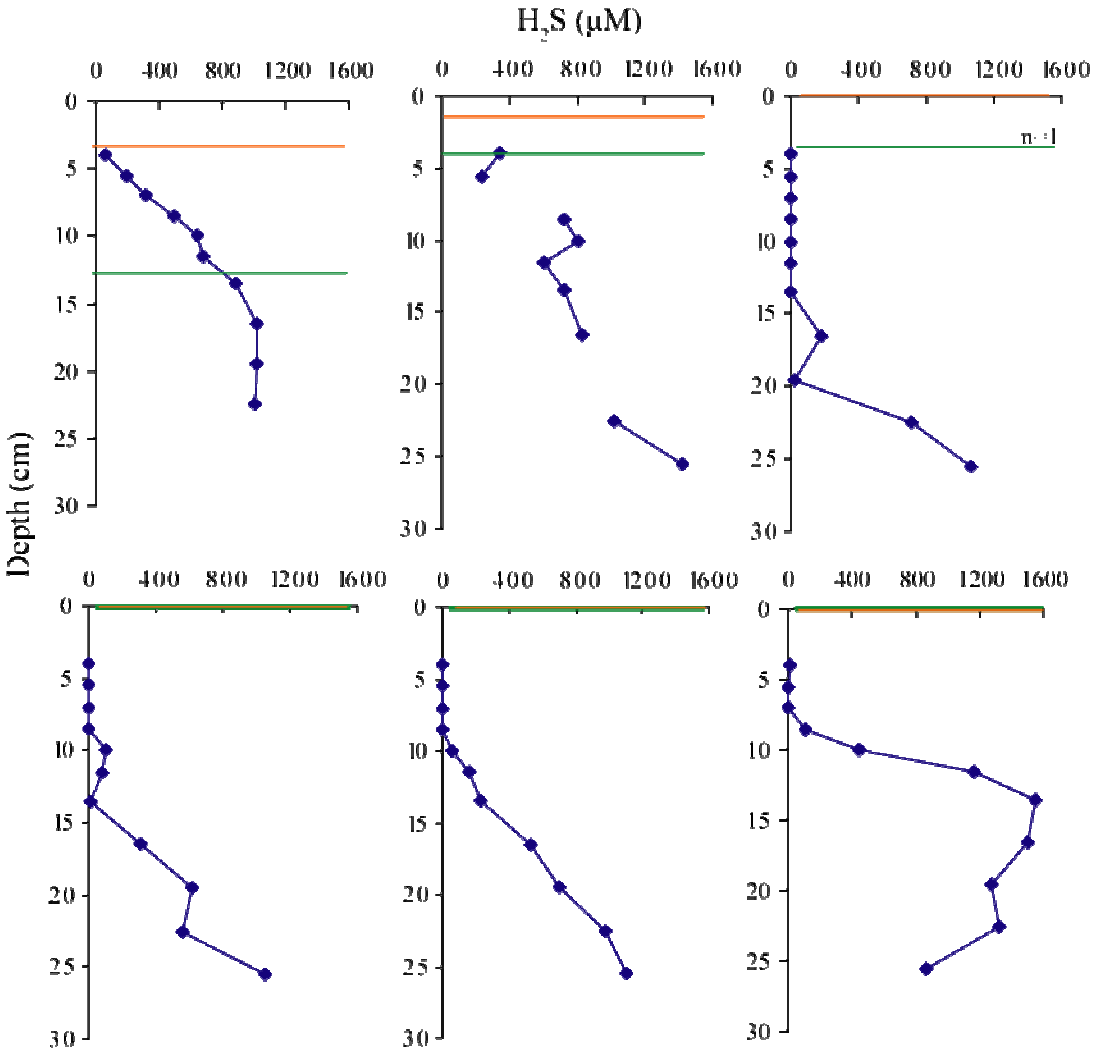


Figure 23: Hydrogen sulfide profiles of locations with old marsh peat (i.e. sand layer < 5 cm) at Mill's Island in June 2005. Green lines represent maximum root length and orange lines represent sand layer depth at each location. Note that n=1 in top right graph represents a mostly unvegetated site with one clump of seagrasses.

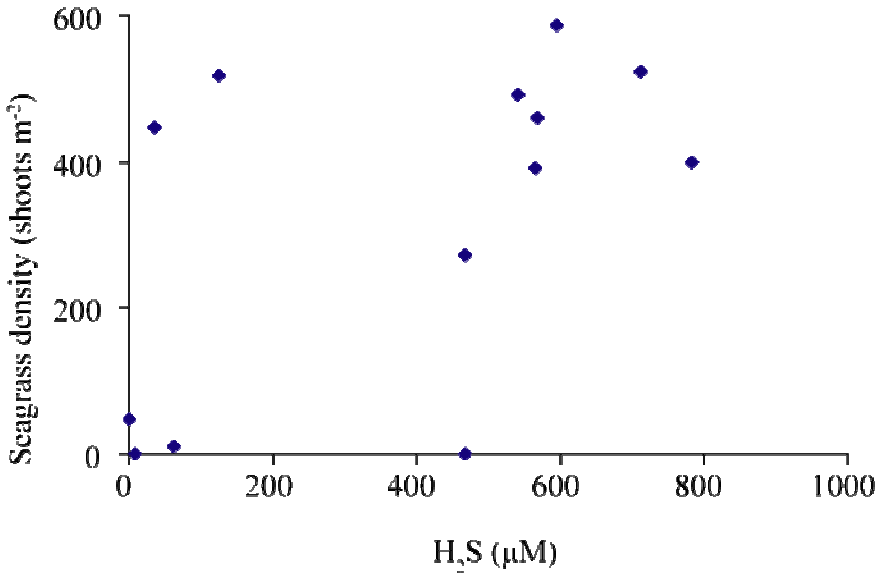


Figure 24: Shoot density of *Zostera marina* compared to hydrogen sulfide concentrations at Mill's Island in June 2005.

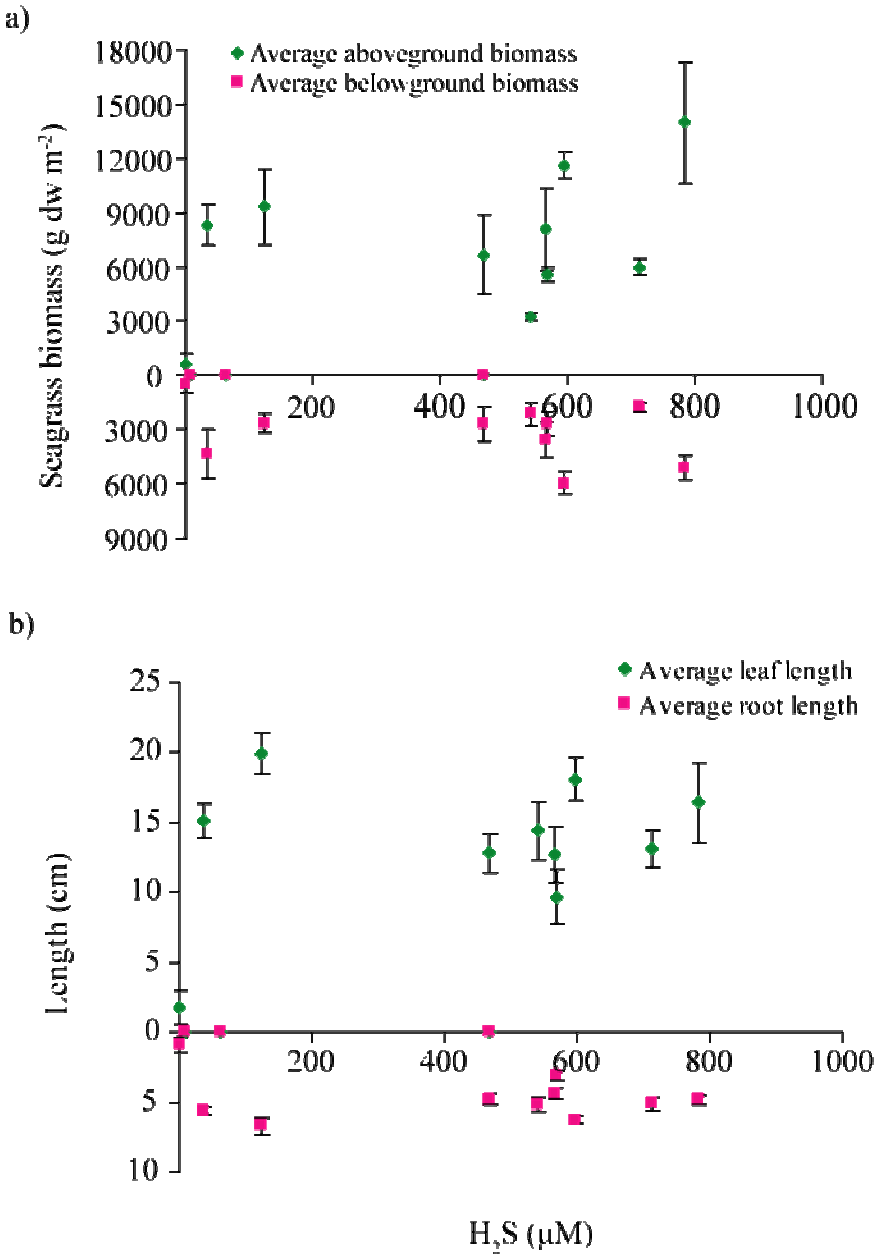


Figure 25: Average aboveground and belowground biomass (a) and average leaf and root length (b) of *Zostera marina* compared to hydrogen sulfide concentrations at Mill's Island in June 2005. Vertical lines represent SE.

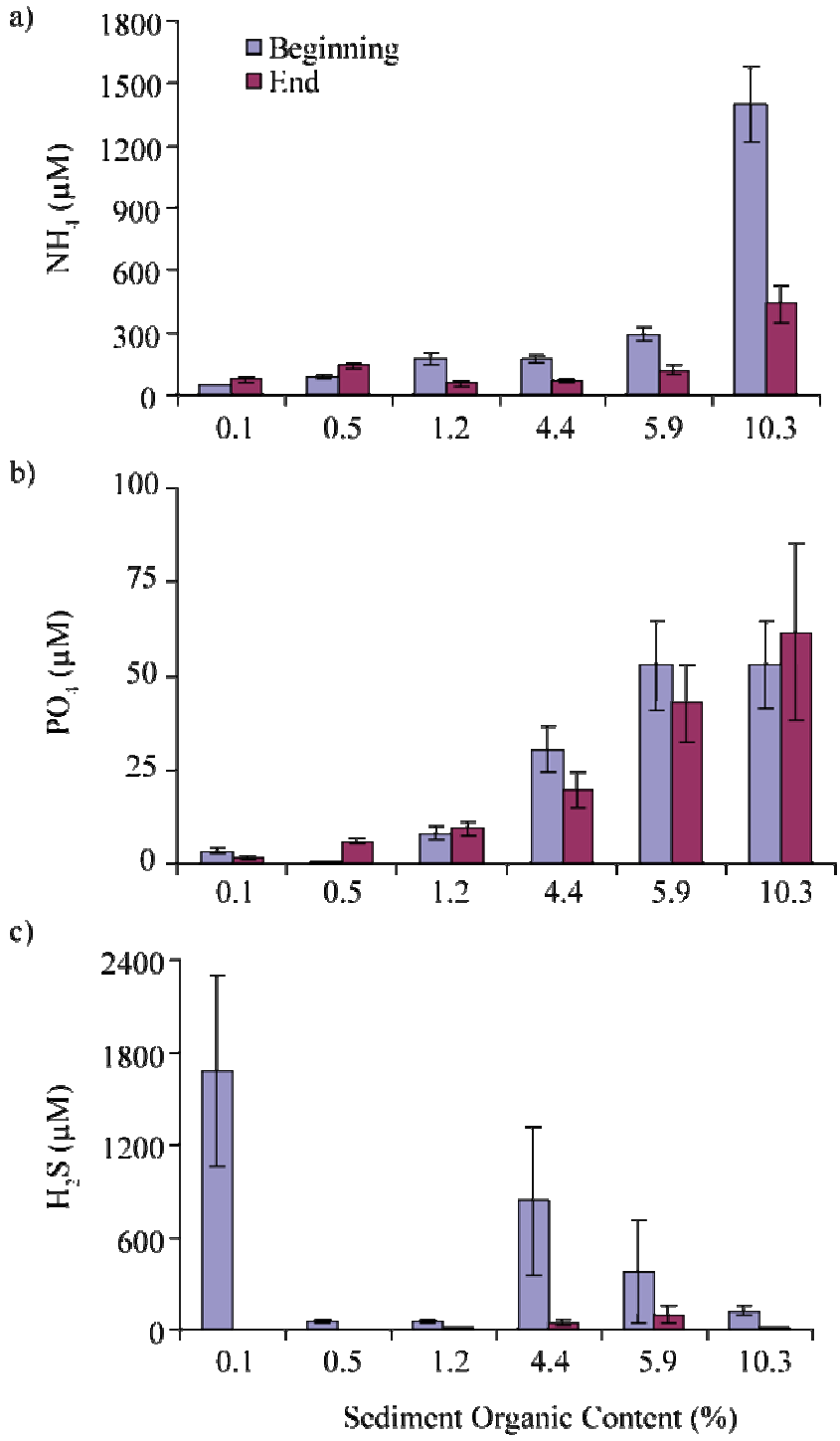


Figure 26: Average concentrations of (a) ammonium, (b) phosphate and (c) hydrogen sulfide for each sediment organic content treatment at the beginning and end (after 8 weeks of *Zostera marina* growth) of the mesocosm experiment. Vertical lines represent SE.

clay. The sediment was a mixture of sand, clay and decaying organic matter. Additionally, high amounts of iron minerals were observed (orange porewater and orange roots) in this treatment throughout the experiment, while no iron minerals were detected in any other treatment at any time during the experiment. This highly organic sediment never compacted, as the other sediments did, and remained in suspension throughout the experiment, which may have resulted in lower sulfide concentrations than the other treatments. Due to these characteristics, the relationship between seagrass growth parameters and porewater nutrients and hydrogen sulfide in the 10.3% organic treatment affected the overall results and conclusions for the entire experiment. Therefore, the results for all treatments as well as for the five lower organic treatments, i.e. excluding the 10.3% organic treatment, are presented.

Porewater ammonium concentrations increased on average between the beginning and the end of the experiment in the 0.1% and 0.5% organic treatments, but decreased in all other treatments (Figure 26a). The 10.3% organic treatment had average ammonium concentrations ranging from 191 to 731 μM at the end of the experiment. All other treatments ranged on average from 21 to 207 μM at the end of the experiment (Figure 26a). Average aboveground (r^2=0.29) and belowground biomass (r^2=0.22) and average leaf length (r^2=0.28) increased with increasing average porewater ammonium concentrations up to 400 μM, then decreased thereafter (Figures 27a and 28a). However, three high ammonium concentrations from the 10.3% organic content treatment were driving the relationship. When only organic contents up to 5.9% were considered, average aboveground biomass (r^2=0.78), average belowground biomass (r^2=0.72) and average leaf length (r^2=0.78) all increased linearly with increasing average porewater

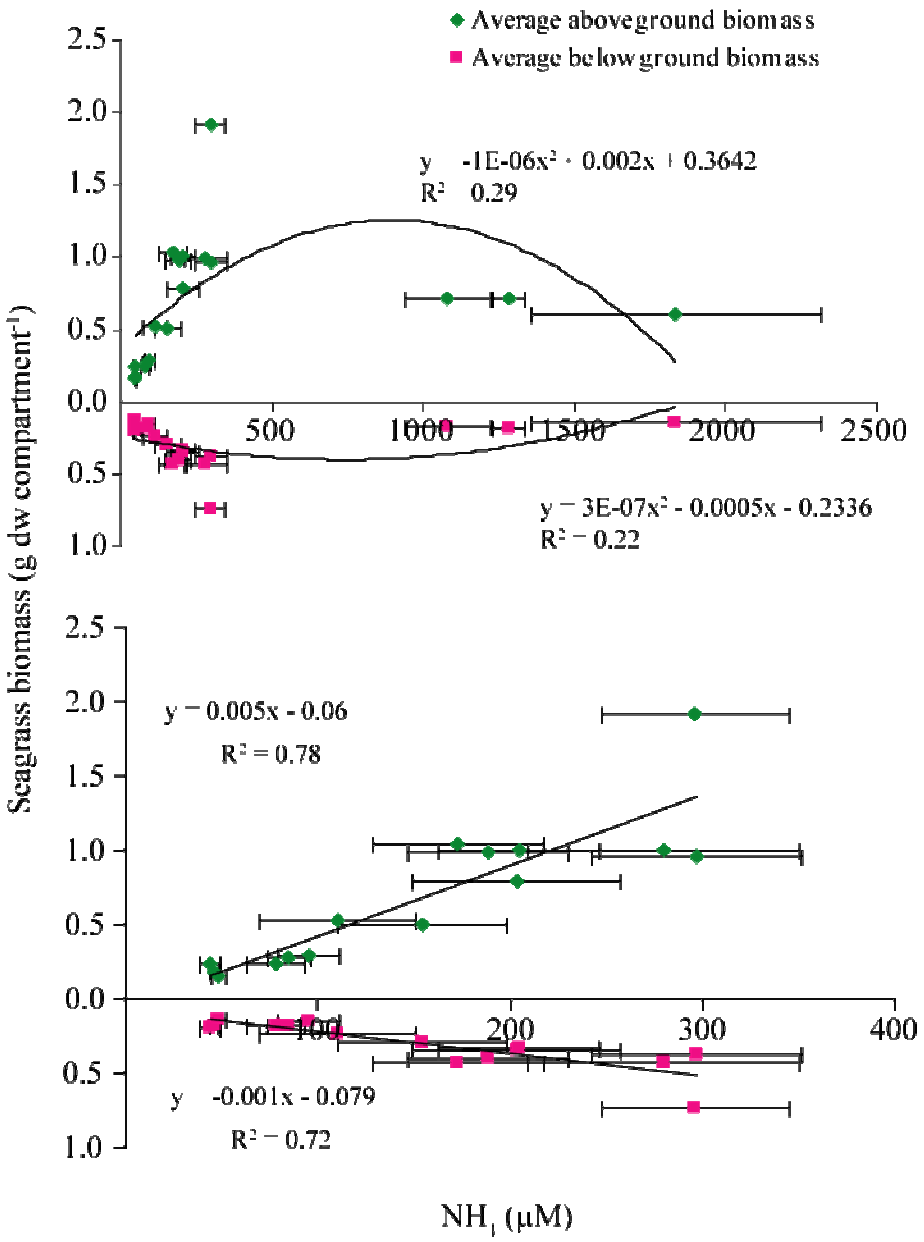


Figure 27: Average aboveground and belowground biomass of *Zostera marina* as a function of porewater ammonium concentrations in a mesocosm experiment with sediment organic contents between 0.1% and 10.3% (a) and 0.1% and 5.9% (b). Horizontal lines represent SE.

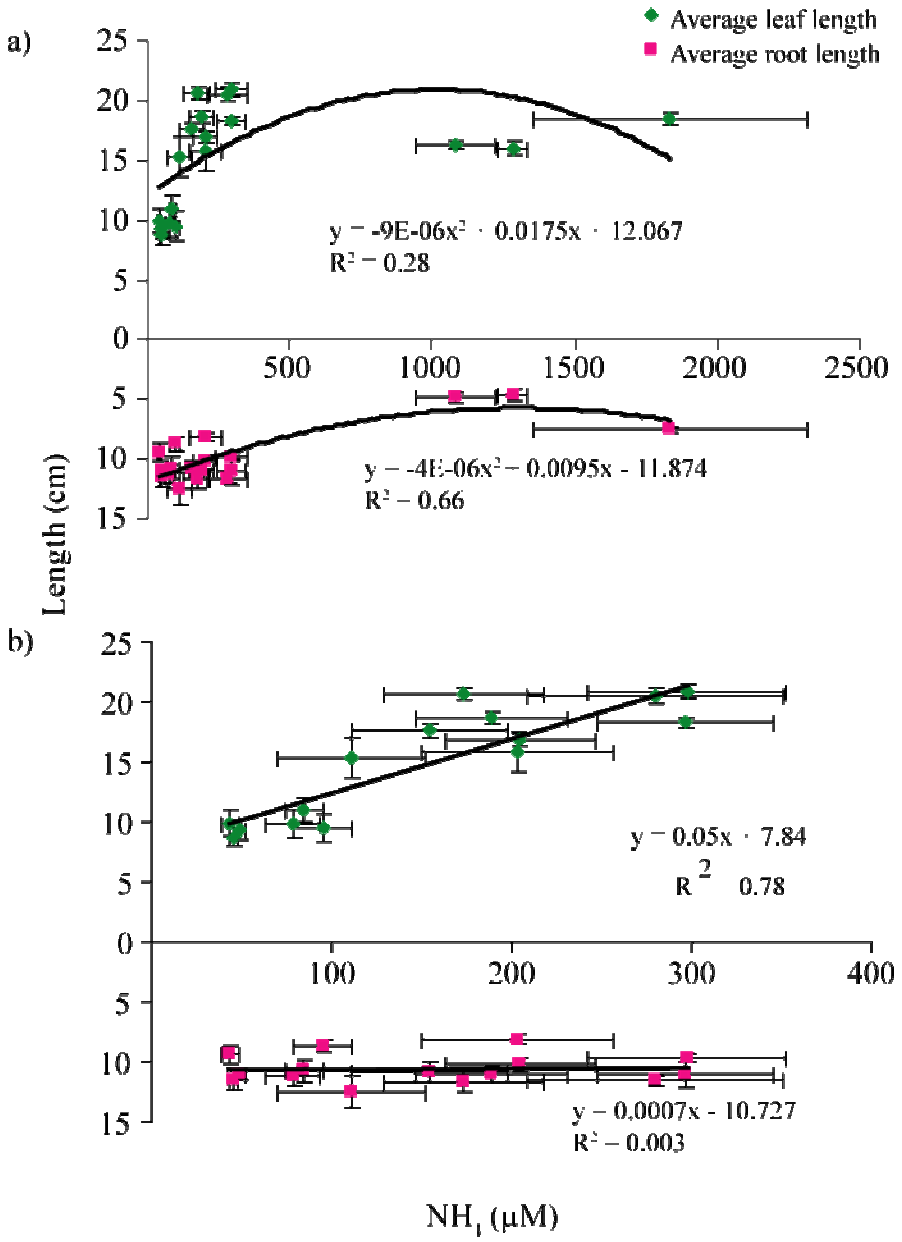


Figure 28: (a) Average leaf and root length of *Zostera marina* as a function of porewater ammonium concentrations in a mesocosm with sediment organic contents between 0.1% and 10.3% (a) and 0.1% and 5.9% (b). Horizontal and vertical lines represent SE.

ammonium (Figures 27b and 28b). Average root length showed a negative trend with initial average ammonium concentrations (r^2=0.66, Figure 28a). However, this relationship was determined by the short root lengths in the 10.3% organic content treatment. Average root length showed no trend with average porewater ammonium concentrations in sediment organic contents up to 5.9% (r^2=0.003, Figure 28b).

Between the beginning and the end of the experiment, average porewater phosphate concentrations increased in the 0.5%, 1.2% and 10.3% organic content treatments and decreased in all other treatments. Phosphate concentrations varied within the three highest organic treatments more widely than ammonium concentrations (Figure 26b, SE = 6.0 – 11.9 μM). Contrary to ammonium concentrations, phosphate concentrations in the 10.3% organic treatment were on the same scale as all other treatments (Figure 26b). Average aboveground (r^2=0.49) and belowground biomass (r^2=0.24) showed a positive trend with initial average phosphate concentrations up to 80 μM, but at a decreasing rate (Figure 29a). Average leaf length increased with increasing porewater phosphate concentrations up to 40 μM, then decreased thereafter (r^2=0.78, Figure 30a). Average root length did not show a trend with porewater phosphate concentrations, except for a decrease in root length in the 10.3% organic content treatment (r^2=0.22, Figure 30a). When only organic contents up to 5.9% were considered, average aboveground biomass (r^2=0.70), average belowground biomass (r^2=0.73) and average leaf length (r^2=0.52) all increased linearly with increasing average porewater phosphate (Figures 29b and 30b). There was no trend between average root length and average porewater phosphate (r^2=0.01, Figure 30b).

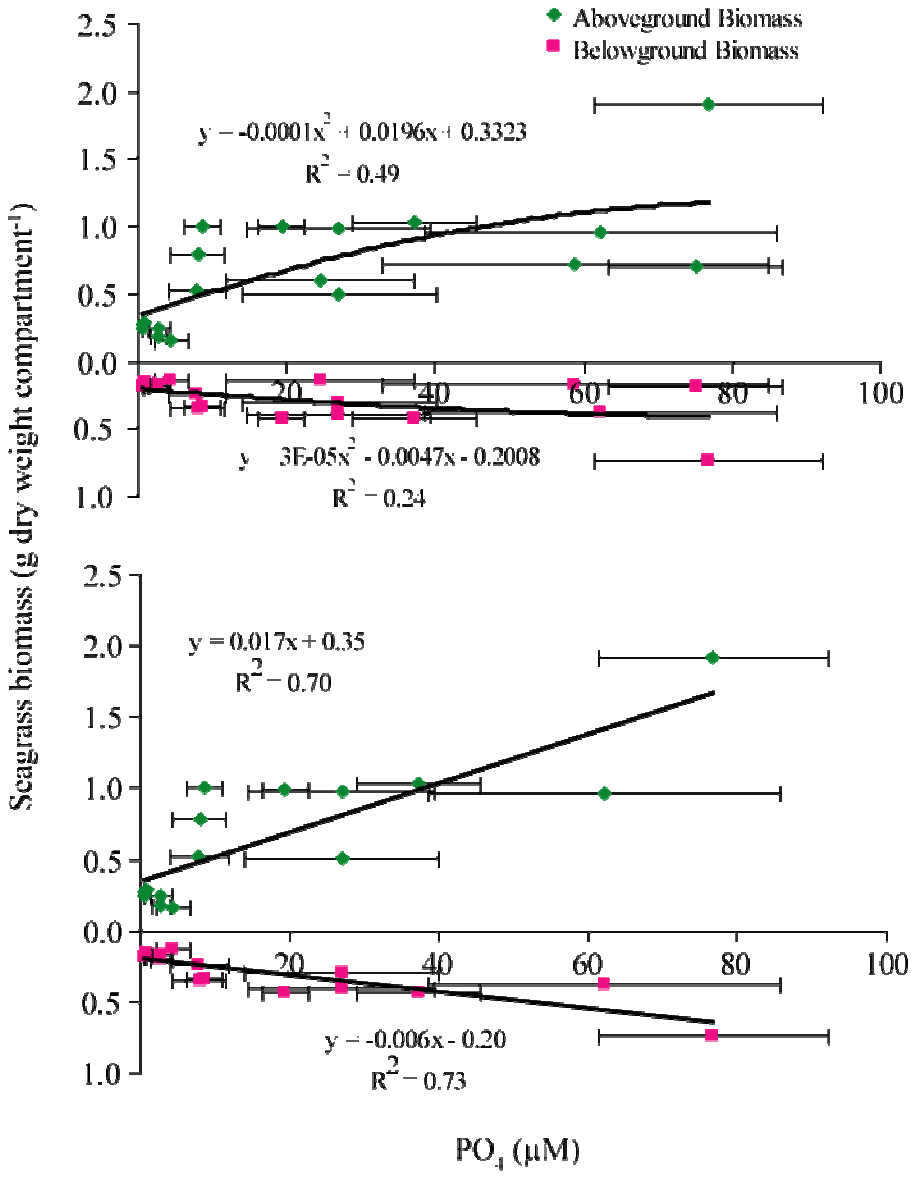


Figure 29: Average aboveground and belowground biomass of *Zostera marina* as a function of porewater phosphate concentrations in a mesocosm experiment with sediment organic contents between 0.1% and 10.3% (a) and 0.1% and 5.9% (b). Horizontal lines represent SE.

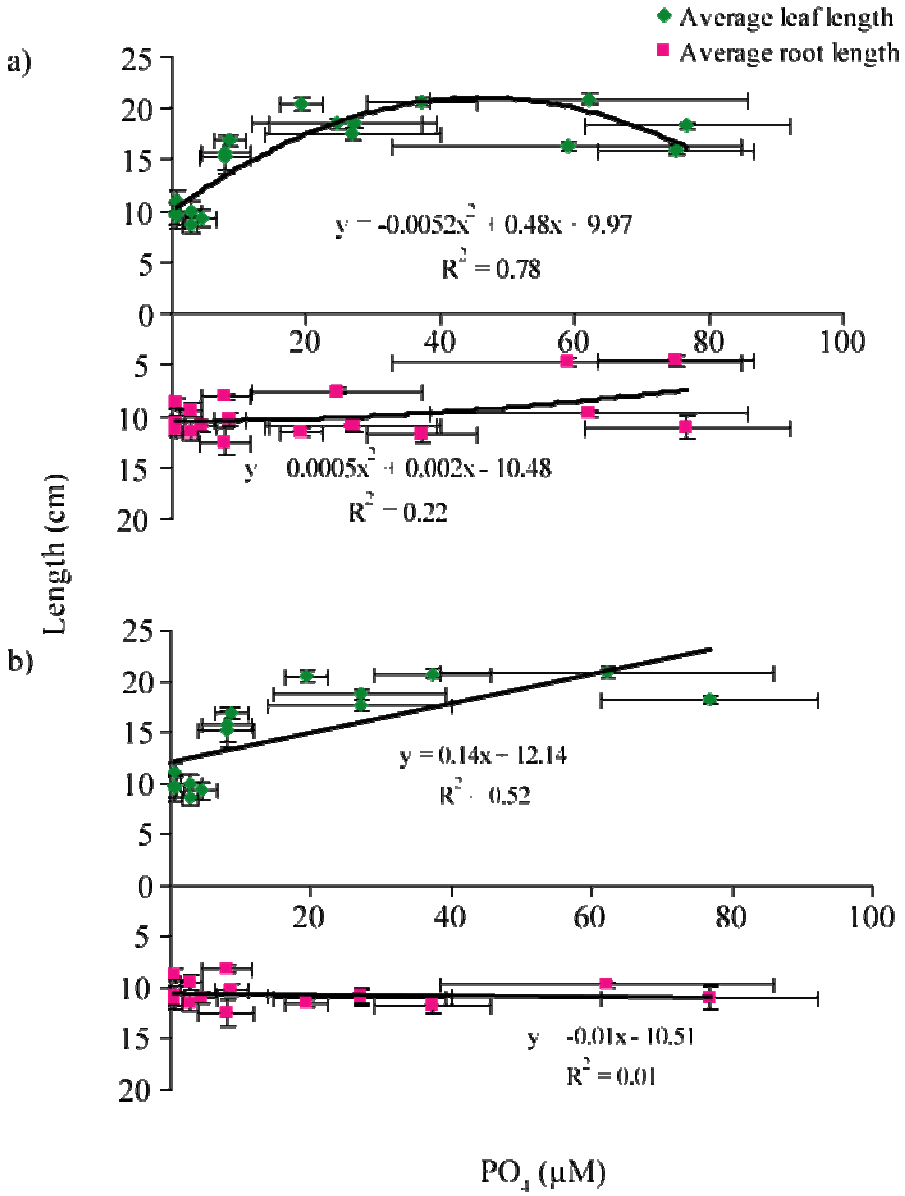


Figure 30: Average leaf and root length of *Zostera marina* as a function of porewater phosphate concentrations in a mesocosm experiment with sediment organic contents between 0.1% and 10.3% (a) and 0.1% and 5.9% (b). Horizontal and vertical lines represent SE.

Porewater hydrogen sulfide decreased over the course of the experiment in all treatments (Figure 26c). There were initially high hydrogen sulfide concentrations in one of the 0.1% organic treatment replicates (greater than 1000 μM, Figure 26c, SE=616 μM). Hydrogen sulfide concentrations were lower in the 10.3% organic treatment than in the 4.4% and 5.9% organic treatments and were most likely a result of the high permeability of the sediment used for the 10.3% organic treatment and/or a result of sulfide reacting with iron to form pyrite (Heijs et al. 1999). Even at average concentrations of 1000 μM or higher, porewater hydrogen sulfide concentrations had no effect on average aboveground and belowground biomass or average leaf and root length (Figure 31a and b).

DISCUSSION

The sediment geochemistry of old marsh peat at Mill's Island is suitable for *Zostera marina* growth: nutrients are readily available (Appendix I) and hydrogen sulfide concentrations are below toxic levels. In contrast, sand seems to be nutrient limiting at times. Ammonium is the primary sediment nutrient that affects *Zostera marina* growth at some locations (Iizumi and Hattori 1982), while phosphorus and iron can be the limiting nutrient at others (Short et al. 1990, Duarte et al. 1995) and porewater phosphate concentrations co-vary with porewater ammonium concentrations (Figure 32). Additionally, seagrass growth parameters followed the same pattern with phosphate as they did for ammonium. Therefore, conclusions drawn for ammonium also apply to phosphate. The controlled mesocosm experiment created porewater concentrations similar to those observed *in situ* (this study) as well as those in other studies (Dennison et

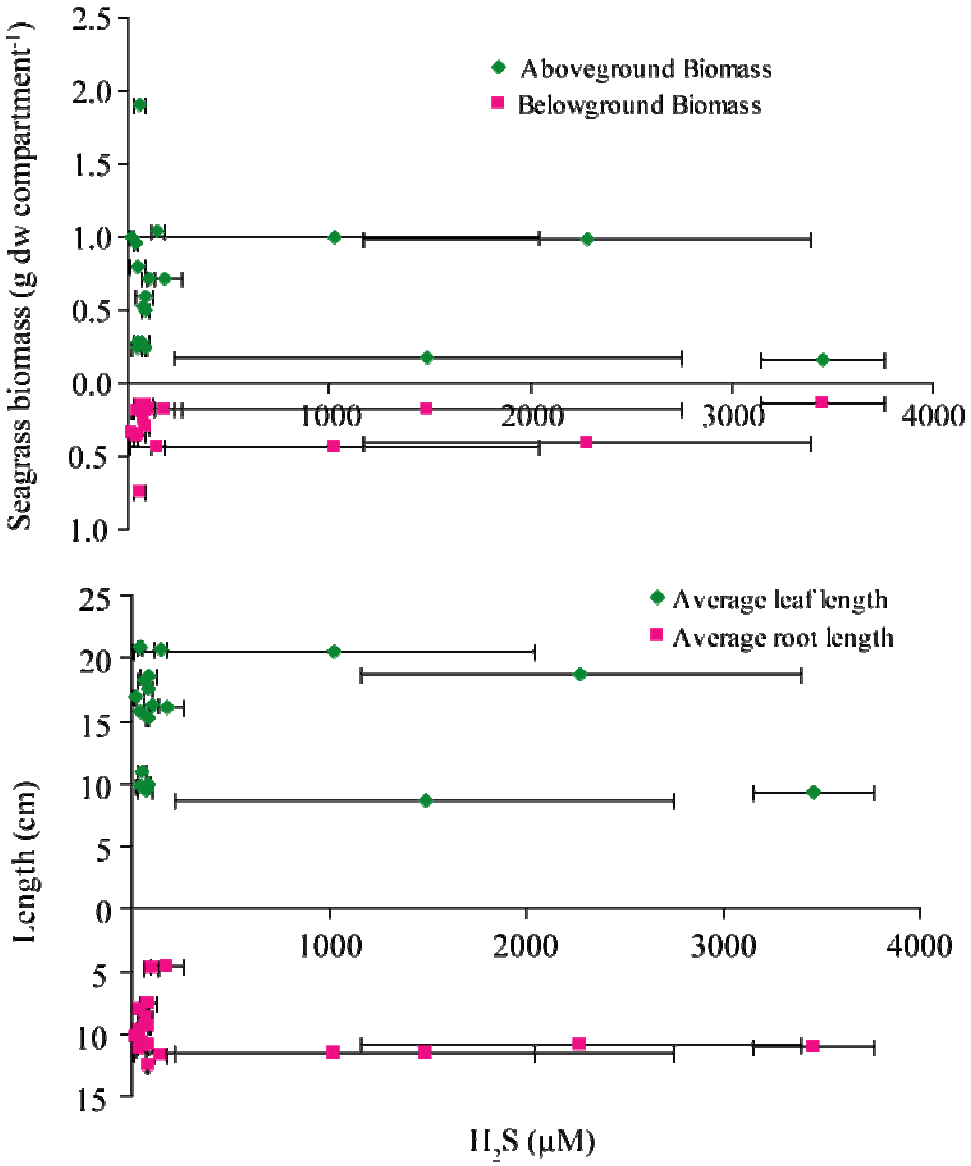


Figure 31: Average biomass and leaf and root length of *Zostera marina* compared to porewater hydrogen sulfide in a mesocosm with sediment organic contents between 0.1% and 10.3%. Horizontal lines represent SE.

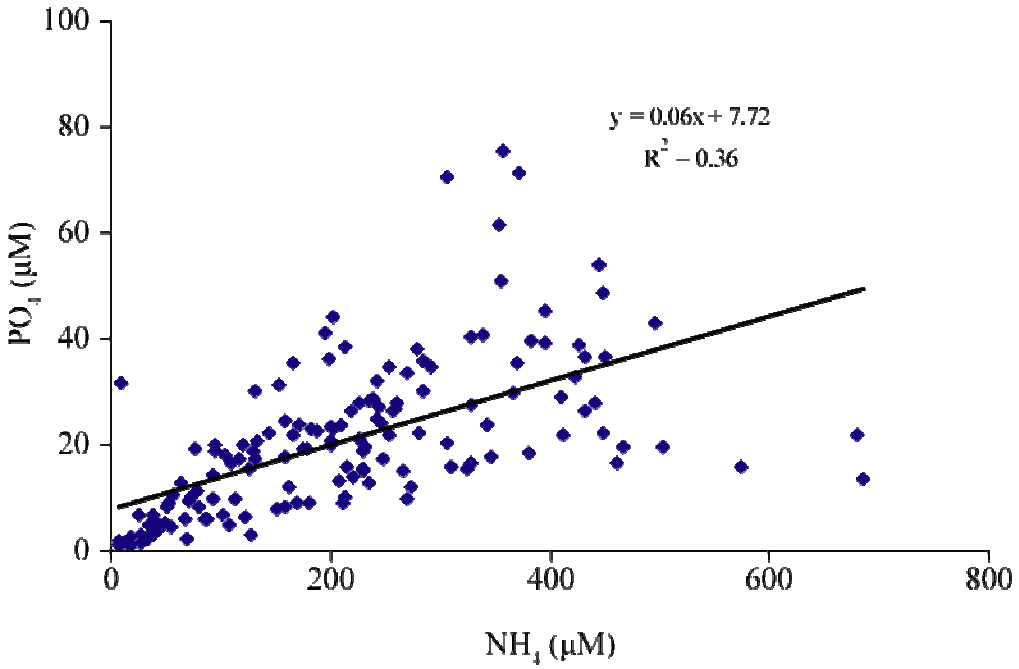


Figure 32: Porewater phosphate concentrations covary with porewater ammonium concentrations at Mill's Island (y = 0.06x + 7.72).

al. 1987, Murray et al. 1992, Peralta et al. 2003). Porewater ammonium concentrations found in old marsh peat are sufficient to support extensive seagrass growth, but as previously reported by Short (1987), sandy sediments may be nutrient limiting in the organic poor sand treatments. Even this reduced biomass may still be an overestimation of growth in organic poor sediments as it appears that water column nutrients were advected into the sand (e.g. Koch and Huettel 2000), as suggested by the increase in ammonium from the beginning to the end of the experiment. Remineralization can also affect the available nutrient supply (Miyajima et al. 2001, Gacia et al. 2002), but remineralization rates were not measured in this experiment.

The findings from the mesocosm experiment are not supported by the results *in situ*. Seagrass shoot density did not show a trend with ammonium concentrations. Seagrass biomass did not show a trend with ammonium concentrations up to 200 μM, suggesting that (a) seagrass shoot density and biomass *in situ* were not nutrient limited in sand and (b) ammonium concentrations were sufficient for seagrass growth in old marsh peat. As seagrasses can take up nutrients through the leaves as well as the roots, nitrogen limitation may not be occurring at Mill's Island due to water column nutrients being sufficient for growth (Williams and Ruckelhaus 1993, Touchette and Burkholder 2000, Wazniak et al., in press). Seagrass shoot density seemed to plateau above 100 μM and aboveground and belowground biomass seemed to decrease above ammonium concentrations of 200 μM, suggesting saturating levels of ammonium may have been reached (Dennison et al. 1987).

Both the field and mesocosm data showed that porewater hydrogen sulfide is not limiting seagrass growth in sediments adjacent to retreating marshes. While it was

expected that hydrogen sulfide levels would be low in the sand and increase in the old marsh peat (Brueechert and Pratt 1996, Holmer and Laursen 2002), this was not consistently the case at Mill's Island. There were several sampling sites where hydrogen sulfide was at medium levels in the sand (up to 1200 μM to depths of 25 cm, up to 800 μM in the top 10 cm) and at low levels (0 – 1000 μM to depths of 25 cm) in the old marsh peat. *Zostera marina* shoot density and leaf and root length in the field and in the mesocosm did not show a trend with hydrogen sulfide, supporting the findings that sulfide is not limiting seagrass growth in sediments adjacent to retreating marshes. Perhaps the best observation to support this conclusion comes from the fact that hydrogen sulfide concentrations were highest in the old marsh peat treatments in the mesocosm experiment, which were also the treatments with highest growth.

Several studies corroborate with the present study that hydrogen sulfide alone does not decrease seagrass growth (Goodman et al. 1995, Koch and Erskine 2001, Eldridge et al. 2004, Holmer et al. 2005). However, they do illustrate the fact that parameters controlling seagrass growth in nature are synergistic and difficult to separate. An enrichment study in Chincoteague Bay showed that maximum photosynthesis of *Zostera marina* decreases with increasing sulfide concentrations (100 – 1000 μM) and low light (Goodman et al. 1995). This scenario is best applied to eutrophic systems and can eventually lead to the loss of vegetation (Goodman et al. 1995). Furthermore, a stress response model for *Thalassia testudinum* in Lower Laguna Madre, Texas, demonstrated that increased algal blooms (associated with eutrophication) can lead to increased sediment sulfides (via organic matter input), which in turn decreases seagrass biomass and makes it difficult for the beds to recover (Eldridge et al. 2004). While eutrophication

is not currently an issue in the lower part of Chincoteague Bay (Wazniak et al. 2004), recent monitoring has suggested that water quality is starting to decline (Wazniak et al., in press). While hydrogen sulfide is not limiting seagrass shoot density, biomass or leaf and root length at Mill's Island at present, if degradation of the water quality in Chincoteague Bay continues, the combination of high hydrogen sulfide concentrations and environmental stressors, such as reduced light availability, may be a problem in the future. This should be taken into account when predicting the success of seagrasses adjacent to retreating marshes.

One exception to these findings was that *Zostera marina* biomass increased with increasing hydrogen sulfide concentrations at Mill's Island in 2004. However, this may be a product of the fact that ammonium concentrations co-vary with hydrogen sulfide concentrations (Figure 33), rather than that hydrogen sulfide increases seagrass biomass. Overall, the variability of ammonium concentrations increased with increasing hydrogen sulfide concentrations. At hydrogen sulfide values less than 400 μM, a threshold above which photosynthesis may begin to be affected (Goodman et al. 1995), ammonium concentrations were low, with a few exceptions. Between hydrogen sulfide concentrations of 400 and 1000 μM, a threshold above which mortality may occur (Kemp et al. 2004), ammonium concentrations had a larger range of variability, while hydrogen sulfide continued to increase. At hydrogen sulfide concentrations above 1000 μM, i.e. likely to be toxic to seagrasses, ammonium concentrations leveled off, possibly due to rapid nitrogen cycling in the sediments (O'Donohue et al. 1991, McGlathery et al. 1998). Hydrogen sulfide concentrations never reached toxic levels in the rhizosphere, even at locations where the sediment type of the rhizosphere was old marsh peat.

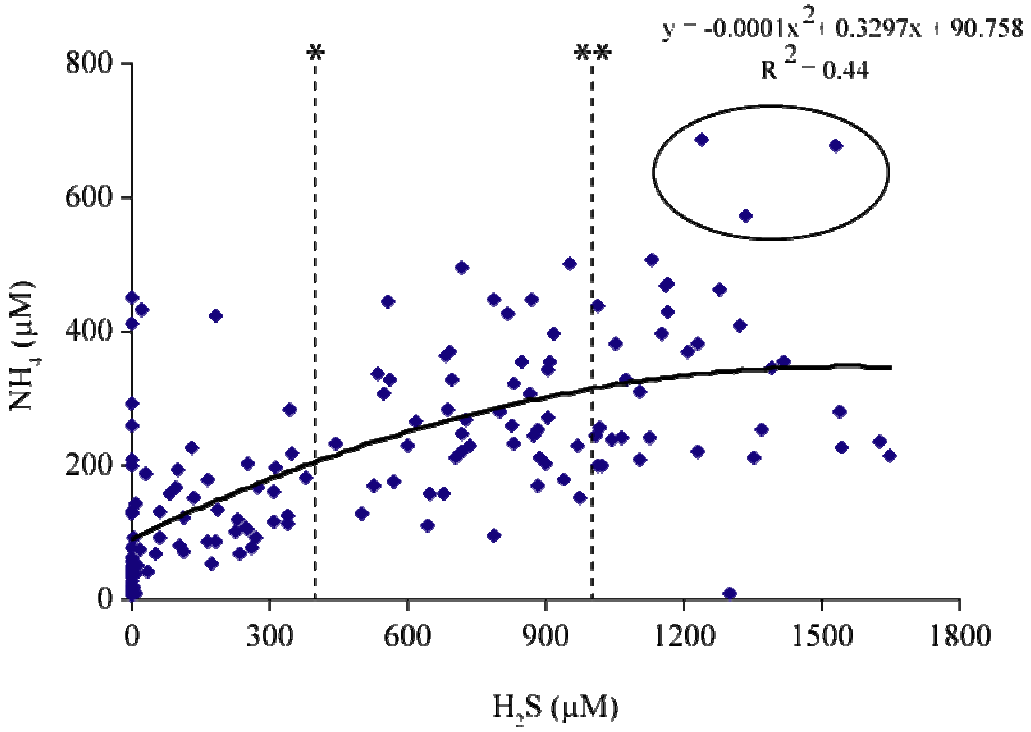


Figure 33: Porewater ammonium covaries with porewater hydrogen sulfide at all depths sampled (up to 25 cm) at Mill's Island. * 400 µM H_2S has been suggested to decrease seagrass photosynthetic capacity (Goodman et al. 1995). ** 1000 µM H_2S has been suggested to decrease seagrass growth (Kemp et al. 2004). The circled points are from the same profile. where ammonium and hydrogen sulfide levels spiked below the rhizosphere.

In summary, the sediment geochemistry of old marsh peat characteristic of subtidal habitats adjacent to retreating marshes is suitable for seagrass growth. While there were some contrasting results between the mesocosm and the field data (i.e. nutrient limitation in sand in the mesocosm, but not in the field), overall the ammonium concentrations in both were within the range reported for other studies (Dennison et al. 1987, Short 1987, McGlathery et al. 1998). Due to the fact that (1) seagrasses grew best in old marsh peat treatments in the mesocosm experiment, (2) seagrasses grew in sand and sand overlaying old marsh peat and (3) there was no clear trend between seagrass growth and ammonium concentrations *in situ*, it seems that ammonium concentrations are not determining presence/absence of seagrasses in sediments adjacent to retreating marshes and that ammonium is more than sufficient for seagrass growth. This is confirmed by seagrass tissue analysis (Appendix I). Hydrogen sulfide did not decrease seagrass growth in the mesocosm experiment nor *in situ*. Hydrogen sulfide concentrations in sand and old marsh peat did not reach toxic levels (1000 μM, Kemp et al. 2004) in the rhizosphere. While hydrogen sulfide has been found to decrease growth in other studies (Goodman et al. 1995, Koch and Erskine 2001), it was in combination with environmental stressors, such as reduced light availability and elevated temperatures, and caused a synergistic, negative effect on seagrass health. Due to the lack of trends between seagrass growth and hydrogen sulfide in the mesocosm experiment and *in situ*, it appears that hydrogen sulfide is not limiting seagrass growth in sediments adjacent to retreating marshes. Additionally, detrimental effects of high hydrogen sulfide concentrations in combination with environmental stressors is not occurring at Mill's Island because these stressors are absent from the sampling location in

Chincoteague Bay at this time. Despite the geochemistry of old marsh peat being suitable for seagrass growth, they were still absent from areas where sand was not overlaying old marsh peat. One possible cause may be that the high energy environment at Mill's Island (as seen by the retreating shorelines) in combination with decreased anchoring capacity (via plant morphology) is limiting seagrasses in old marsh peat (see Chapter 1).

Chapter 3

Sand overlaying old marsh peat: the key to seagrass growth adjacent to retreating marsh shorelines.

INTRODUCTION

Habitat requirements of *Zostera marina* include 20% of surface irradiance, gentle current velocities and mild wave action (Sullivan and Titus 1966, Ackerman 1986, Dennison et al. 1993). Additionally, nutrients in the water column need to be high enough to support growth but low enough to prevent epiphytic growth on the seagrass leaves (Bulthuis and Woelkerling 1983, Lapointe et al. 1994, Hemminga and Duarte 2000). While many studies have focused on light (Dennison 1987, Dennison et al. 1993, Livingston et al. 1998) and water quality (Stevenson et al. 1993, Meyercordt and Meyer-Reil 1999, Tomasko et al. 2001) as the primary parameters affecting seagrass distribution, the sediment environment, which is also important in determining seagrass distribution and colonization, has received less attention (Koch 2001, Kemp et al. 2004). Sediment type, i.e. sand or mud, determines the sediment geochemistry and consequently, seagrass growth (Short 1987, Dennison 1987, Murray et al. 1992, Chapter 2). However, few studies have been performed to determine why seagrasses grow in certain kinds of sediment but not others. The studies that have been performed have focused on sediment nutrients (Short 1983, Dennison 1987, Murray et al. 1992) or sediment dynamics (Marsden et al. 1979, De Falco et al. 2000, van Keulen and Borowitzka 2003), but not sediment composition. Such data is important for understanding the synergistic effects of sediment type, geochemistry and dynamics on seagrass growth and distribution. Furthermore, few studies have been performed at sites where different sediment types

overlay one another. *Thalassia testudinum* is found growing in circular deposits of marine calcareous sediments overlaying mangrove peat in Biscayne Bay, Florida, and seagrass growth is related to the depth of the sediment overlaying the peat (Zieman 1972). Marsh barrier beaches along Chesapeake Bay exhibit a similar layered sediment profile, in which a layer of sand overlays salt marsh peat (Rosen 1980). Due to sea level rise, the marsh shoreline erodes over time, creating a 30 – 50 cm cliff at the edge of the water. As the marsh retreats, the underlying old marsh peat becomes the available substrate in the subtidal. Old marsh peat is here defined as decomposed marsh peat, i.e. organically rich sediment with a large fraction of silt/clay particles (> 50%), which has compacted over time. Sand brought in via longshore transport can then be deposited on top of the peat (if a source of sand is available), leading to a layered substrate in shallow water habitats. The layering effect that is created by sand overlaying old marsh peat affects the geochemical properties of the sediment and has the potential to affect seagrass growth. Organic poor sand is low in nutrients (Short 1987), while organic rich old marsh peat is high in nutrients (Berner 1977). Additionally, hydrogen sulfide levels vary between these different types of sediments (this study, Chapter 1). The current study describes the effects of sand layer depth on seagrass growth and distribution in sediments adjacent to a retreating marsh barrier.

METHODS

Study site

Mill's Island in Chincoteague Bay (Figure 1) was selected based on the presence of a retreating marsh shoreline with an adjacent seagrass bed. The present study took

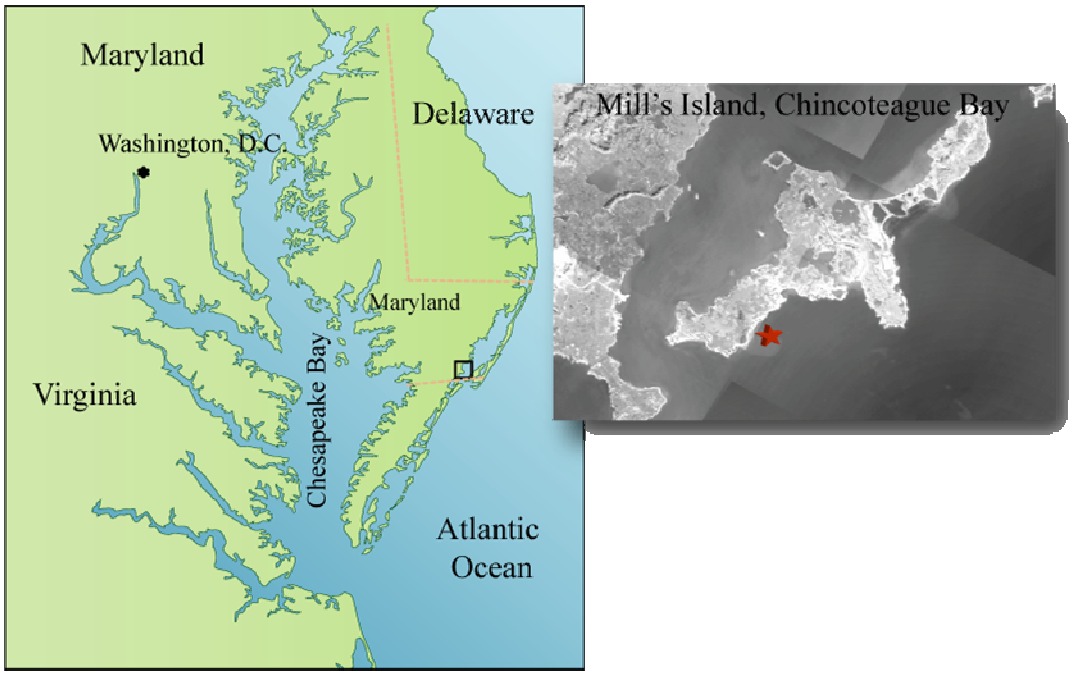


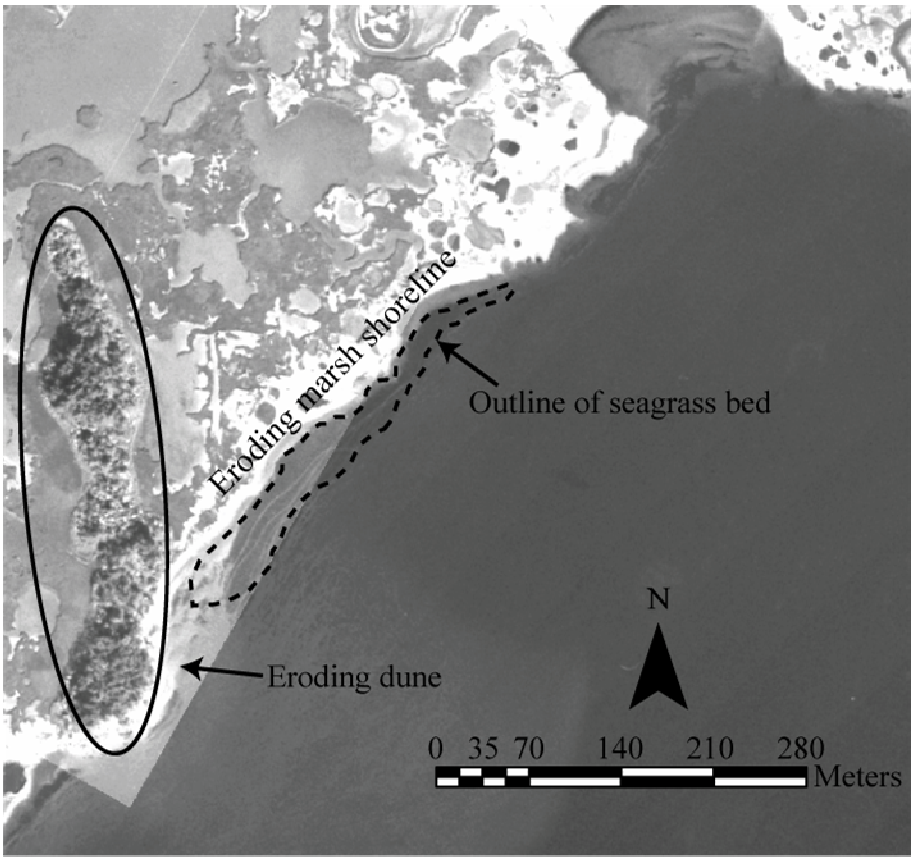
Figure 1: Location of study site ( ) at Mill's Island (38° 03' N, 75° 18' W) in Chincoteague Bay on the Eastern Shore of Maryland.

place at the southeast portion of the island, along a beach extending southwest to northeast. The substrate in the seagrass habitat (i.e. < 1 m water depth) was dominated by old marsh peat along the northeast shoreline and seagrass beds were absent, while the substrate in the seagrass habitat was dominated by a thin sand layer over old marsh peat along the southwest shoreline and seagrass were present (Figure 2). The source of sand was an eroding dune within the marsh system (Figure 2). As the marsh ended in the form of an abrupt scarp, the distance between the erosional marsh shoreline and the shallow edge of the seagrass bed was less than 20 m. The astronomical tidal range at the site was less than 30 cm (NOAA 2005).

Field surveys

In July and August 2004, the waters off the SE shore of Mill's Island were surveyed for seagrass distribution along two transects. Surveys and aerial photographs showed the seagrass bed to be narrow and to follow the shoreline. The outer transect started at the base of the erosional dune and ran northeast, ending beyond the edge of the seagrass bed (Figure 3). This transect length was 340 m and covered the southwest and northeast edges of the seagrass bed. The inner transect was parallel to the outer transect but 20 m closer to shore (Figure 3). The inner transect was 320 m long, covered the entire length of the seagrass bed and ended at the edge of the marsh. Along each transect, GPS coordinates (Garmin International, Inc. eTrex, ± 3 m), water depth (meter stick), seagrass species and shoot density (25 x 25 cm quadrat) were quantified every 10 m. Sediment samples (core = 5 cm in diameter) were also taken every 10 m to determine the thickness of the sand overlaying the old marsh peat. Using the same cores, additional sediment samples were collected every 20 m. The sand and old marsh peat layers in

a)



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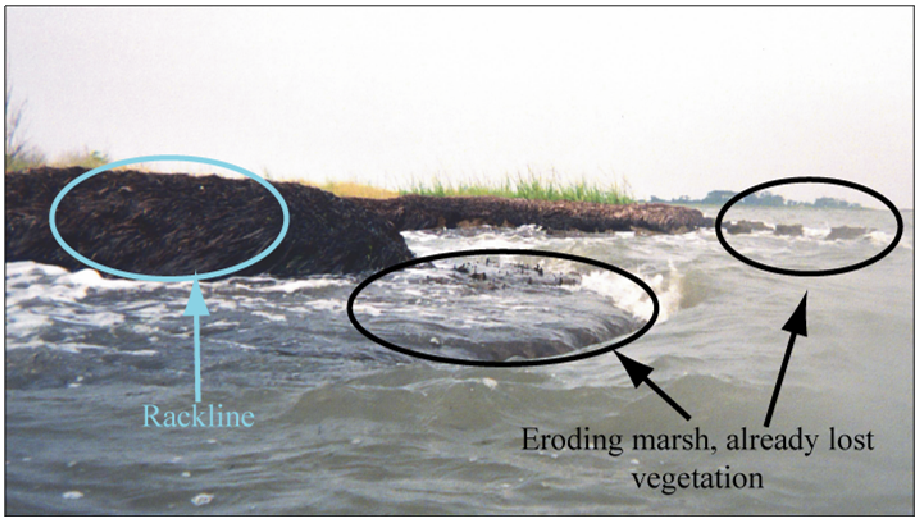

Figure 2: Location of the *Zostera marina* bed and eroding Pleistocene dune at Mill's Island. Chincoteague Bay. Maryland (a). Edge of the seagrass bed was determined by visually assessing a 2003 aerial photograph (courtesy of VIMS) for change in color between bed and bare sand. Photograph of eroding marsh shoreline at Mill's Island (b). Note the process of marsh retreat: marsh erodes from top and edge forming unvegetated platforms that continue to erode until flush with the seafloor.

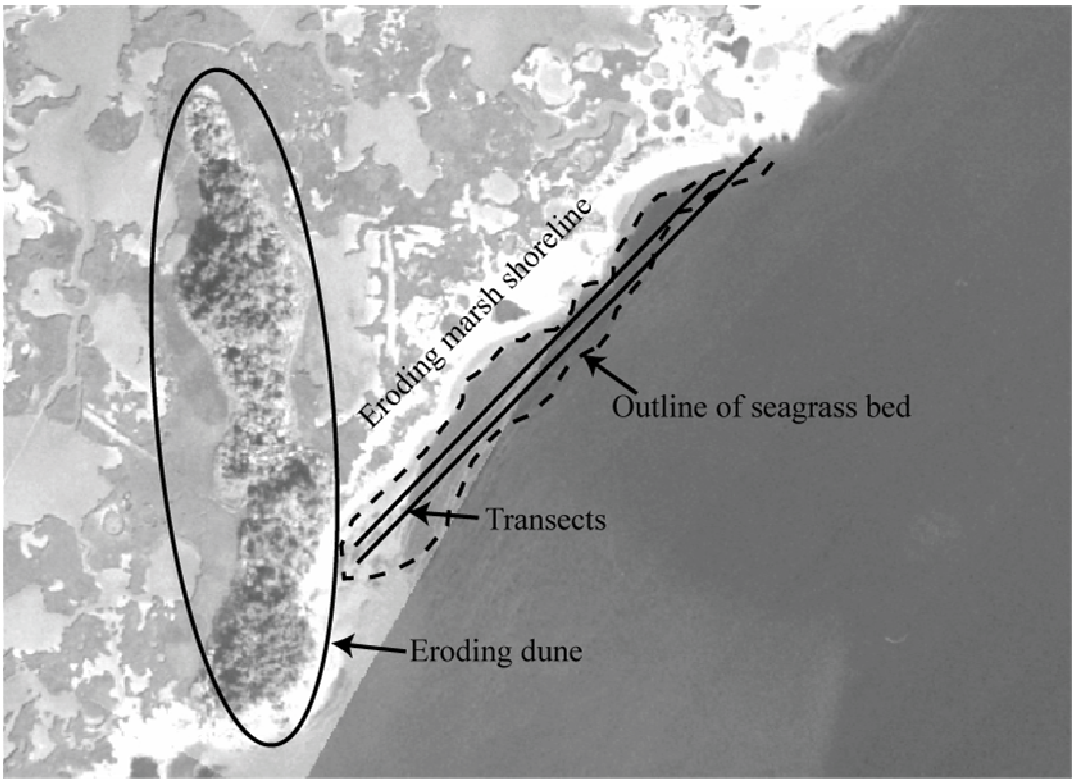

Figure 3: Transect lines for the 2004 survey of a *Zostera marina* bed at Mill's Island, Chincoteague Bay, Maryland. The 2005 survey followed the 80 cm depth contour in proximity of the 2004 inner transect.

these cores were separated based on differences in grain size and sediment color, with the sand having a higher percentage of large grain sizes than the old marsh peat. The different layers were then put in separate, labeled plastic bags and taken to the lab for characterization of grain size according to Erftemeijer and Koch (2001).

In order to determine the relationships between plant biomass, leaf and root length and sand layer depth, seagrass samples were taken at pre-selected locations along each transect in late October, 2004. These locations represented the range of sediment (sand, old marsh peat and sand overlaying old marsh peat) and seagrass (vegetated and unvegetated) combinations found at Mill's Island (Table 1). At each location, three samples of seagrasses were collected with a 5 cm-diameter core within 50 cm of where sediment cores were taken during the previous summer and combined into one sample per location. Prior to combining samples in one bag, all plant material was rinsed in seawater in a sieve to remove any sediment attached to the roots and rhizomes. Samples were refrigerated (6˚ C) until leaf and root length were measured (within 4 wks) via direct measurement using a ruler. Once length measurements were complete, samples were placed in a drying oven (50˚ C), dried to constant weight and weighed to determine biomass.

In June 2005, the field survey was repeated to gather more detailed data on the relationship between plant biomass, leaf and root length and sediment characteristics. While the previous year's data showed a possible relationship between plant growth parameters and sediment organic content, there were not enough samples to make a definitive statement about whether sediment organic content in sediments adjacent to retreating marshes is limiting seagrass growth. However, instead of two straight transects

Inner Transect	
Sand layer depth	Seagrass Present?
> 30 cm	Yes
> 30 cm	No
< 10 cm	Yes
< 10 cm	Yes
Outer transect	
Sand layer depth	Seagrass Present?
> 25 cm	No
> 20 cm	Yes
> 20 cm	Yes
20 cm	Yes
5 cm	No
0 cm	No

Table 1: Description of locations chosen for biomass sampling at Mill's Island in 2004.

through the seagrass bed, fifteen points along a transect at the 80 cm depth contour were sampled, thereby eliminating depth as a co-variable. Seagrass and sediment samples were collected and processed the same way as in the previous year. However, the three seagrass samples taken at each location were kept separate as subsamples rather than combining all into one sample.

Sand layer depth experiment

To determine whether the application of sand over old marsh peat would be a viable technique to restore seagrass beds adjacent to retreating marshes an experiment was run under controlled conditions. Sediment cores (52 cm long, 5 cm in diameter) with a gradient of depths of sand overlaying old marsh peat were placed in an environmental chamber (18° C, 12 hour photoperiod, light levels > 100 μE). Cores had a total sediment column of 25 cm with 20 cm of water overlaying the sediment. The sand layer treatments above old marsh peat were 0, 1, 5, 10 and 20 cm in thickness, n=6 for 0 cm of sand, n=3 for all other treatments (Figure 4). *Zostera marina* seedlings (n=3 per core) were planted in each core in March, 2005 and allowed to grow for 8 weeks. Water in cores was changed once per week. The top of the cores were covered with parafilm to allow for the transfer of gases while preventing evaporation. At the end of the experiment, plants were carefully removed by washing sediment off in a sieve. Then, plant biomass and length (leaf and root) were determined.

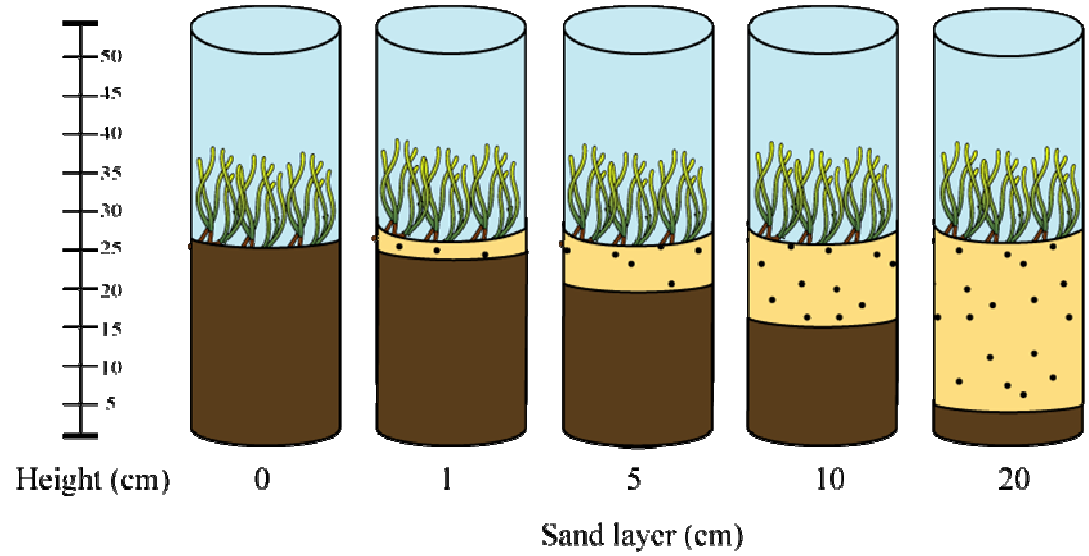

Figure 4: Set up of sand layer experiment. Plants are not a representation of seagrass biomass or height in each treatment. Sand Old marsh peat

RESULTS

Field surveys

Grain size analysis showed that the sand at Mill's Island was composed of mostly fine sand particles and that old marsh peat was composed of mostly silt/clay particles (see Chapter 1). The visual and textural differences between the sediment types were that the sand was grittier to the touch and a different color than the old marsh peat. Additionally, the sand could be separated easily, while the old marsh peat was difficult to break apart. Samples where sand overlay old marsh peat also had a thin mixed layer (~ 1 cm), which had amounts of fine sand to silt/clay in between sand and old marsh peat (see Chapter 1).

In 2004, water depth was a co-variable along the northeast half of the outer transect, but not a co-variable along the inner transect (Figure 5). Seagrass shoot density along the inner transect was not related to sand layer depth (data not shown). Aboveground and belowground biomass tended to increase with increasing sand layer depth up to approximately 6.5 cm, then decreased thereafter (r^2=0.29, r^2=0.37, respectively, Figure 6a). Average leaf and average root length tended to increase with increasing sand layer depth up to approximately 20 cm, then decreased thereafter (r^2=0.62, r^2=0.57, respectively, Figure 6b). However, these results may be misleading as there were only six samples and none had sand layer depths between 6.5 and 19 cm.

In order to obtain a more homogeneous sampling record, the area was resampled in 2005. These data showed an increase in seagrass shoot density with increasing sand layer depth up to approximately 12 cm, then decreased thereafter (r^2=0.88, Figure 7). Average aboveground and belowground biomass increased with increasing sand layer depth, then seemed to plateau at approximately 12 cm (r^2=0.39, r^2=0.56, respectively,

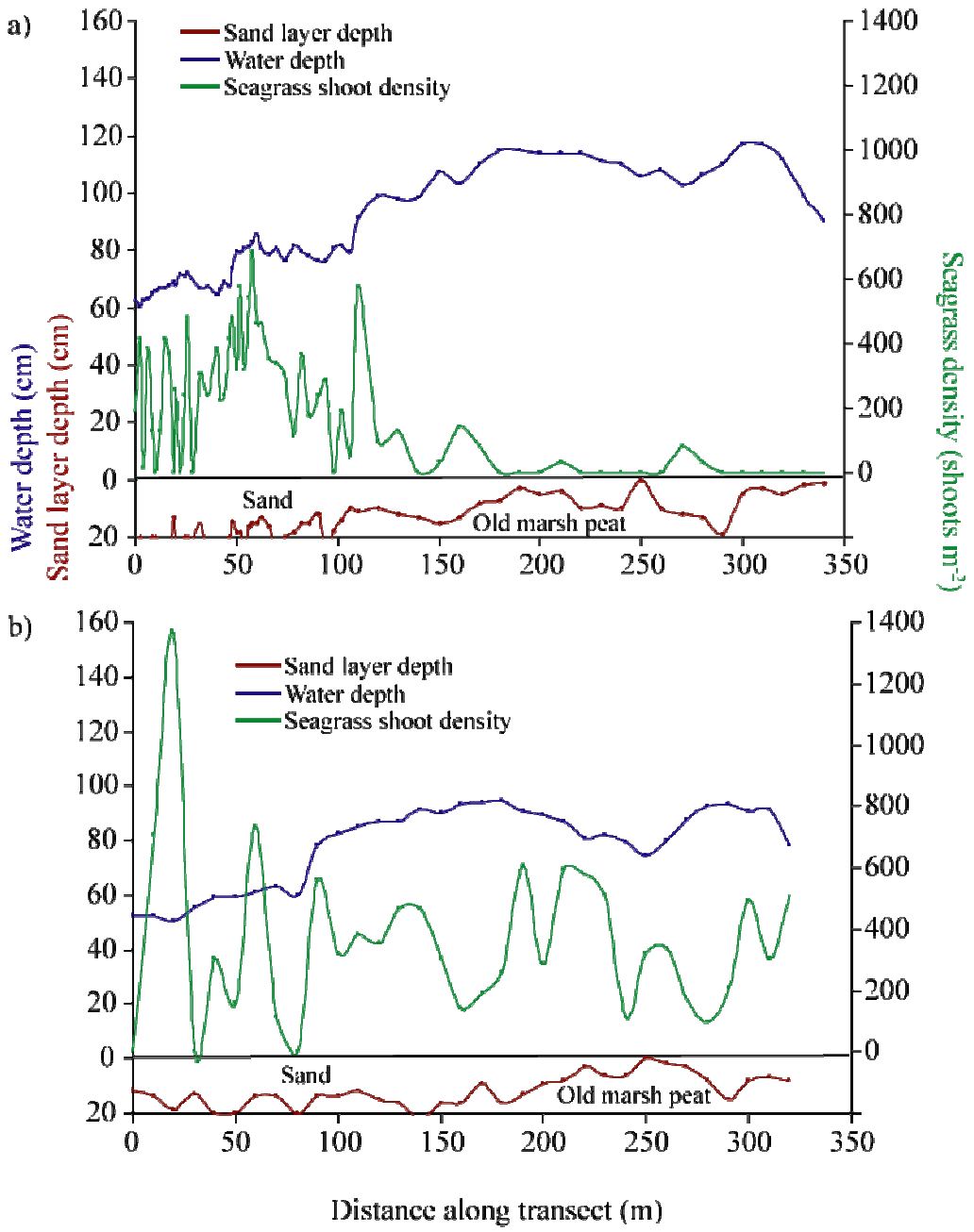

Figure 5: Shoot density of *Zostera marina* and water depth along the outer transect (a) and inner transect (b) at Mill's Island in 2004. Note that water depth and sand layer depth co-varied along the outer transect and seagrasses were mainly absent when water depth > 1 m.

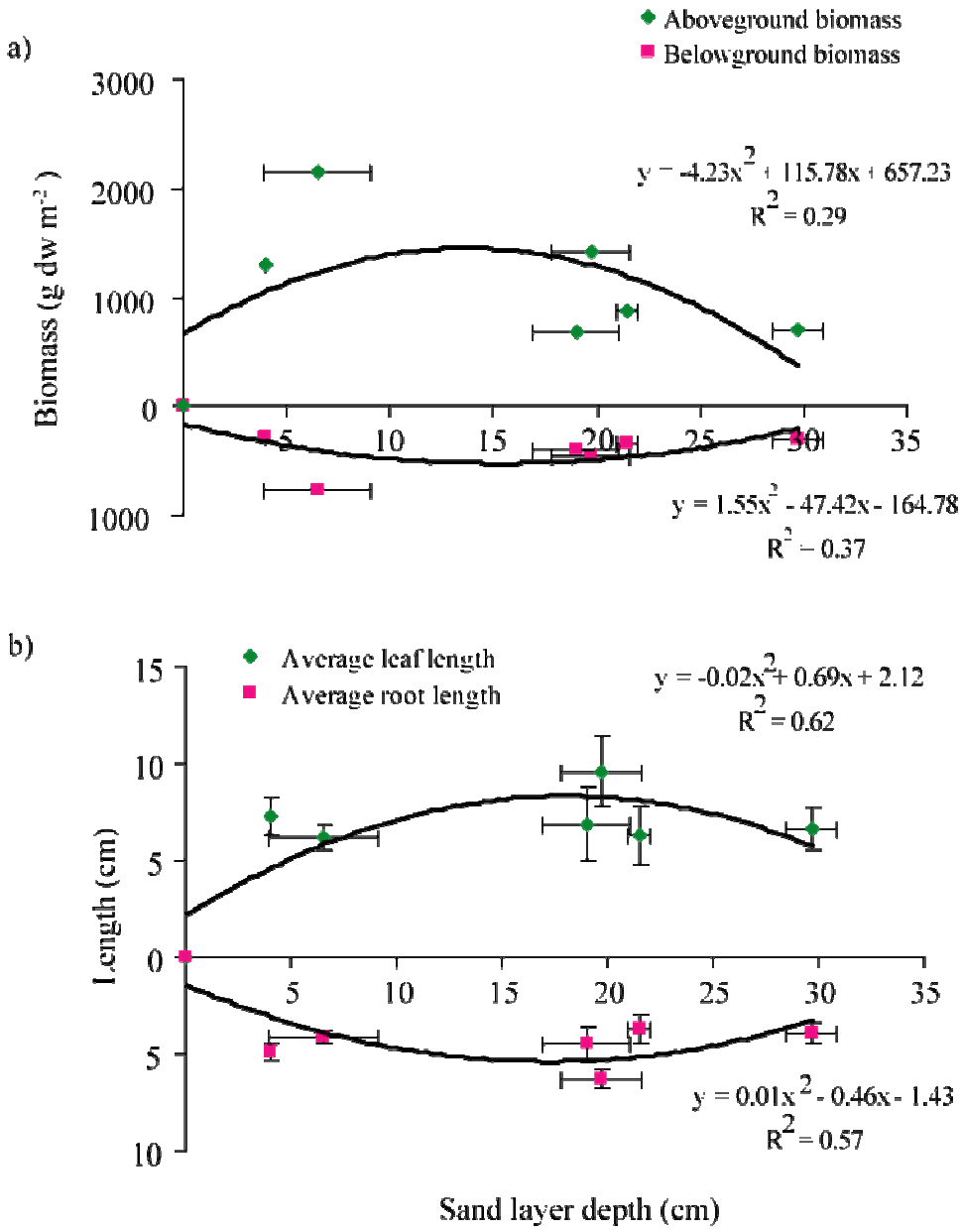

Figure 6: Aboveground and belowground biomass (a) and leaf and root length (b) of *Zostera marina* as a function of sand layer depth from at Mill's Island in 2004. Horizontal and vertical lines represent SE.

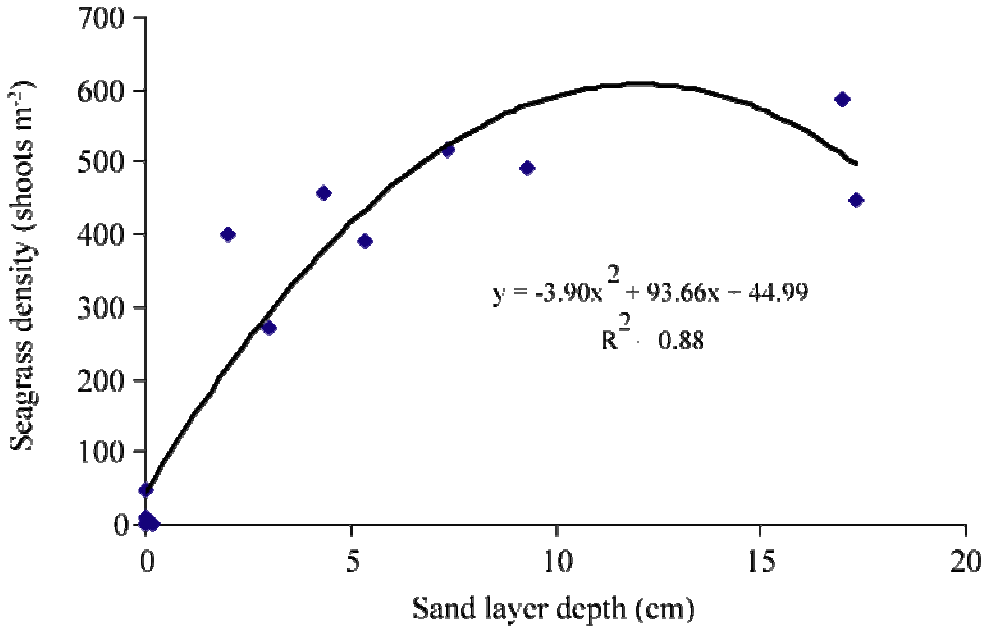

Figure 7: Shoot density of *Zostera marina* as a function of sand layer depth at Mill's Island in 2005.

Figure 8). Average leaf and root length increased with increasing sand layer depth up to approximately 13 cm, then decreased thereafter (r^2=0.77, r^2=0.82, respectively, Figure 9).

Sand layer depth experiment

In the sand layer depth experiment, average aboveground and belowground biomass did not show a trend with sand layer depth (Figure 10). Average leaf and root did not show a trend with sand layer depth, although both tended to decrease slightly with increasing sand layer depth (Figure 11a). The average maximum root length increased with increasing sand layer depth (r^2=0.83, Figure 11b).

DISCUSSION

Sand layer depth appears to be a major factor determining seagrass distribution in sediments adjacent to the retreating marsh at Mill's Island via plant morphology and anchoring capacity. As seen in the sand layer depth experiment, sand layer depth is a primary determinant of root length. With increasing sand layer depth, the roots need to penetrate farther to find adequate nutrients. Therefore, the plants in the 5, 10 and 20 cm of sand treatments were producing longer roots than the plants in the 0 and 1 cm of sand treatments. A relationship between sediment type and plant morphology has been shown in other studies (Short 1983, Lee and Dunton 2000). Contrary to another experiment (Chapters 2 and 3), the plants in the 0 and 1 cm of sand treatments had smaller aboveground biomass in the higher sediment organic content and higher porewater ammonium treatments, i.e. more old marsh peat in the upper 15 cm. The experimental set up may explain the lack of a trend. There was more epiphytic fouling of the cores and plants in treatments with 0 and 1 cm sand layer depth than all other treatments. The cores

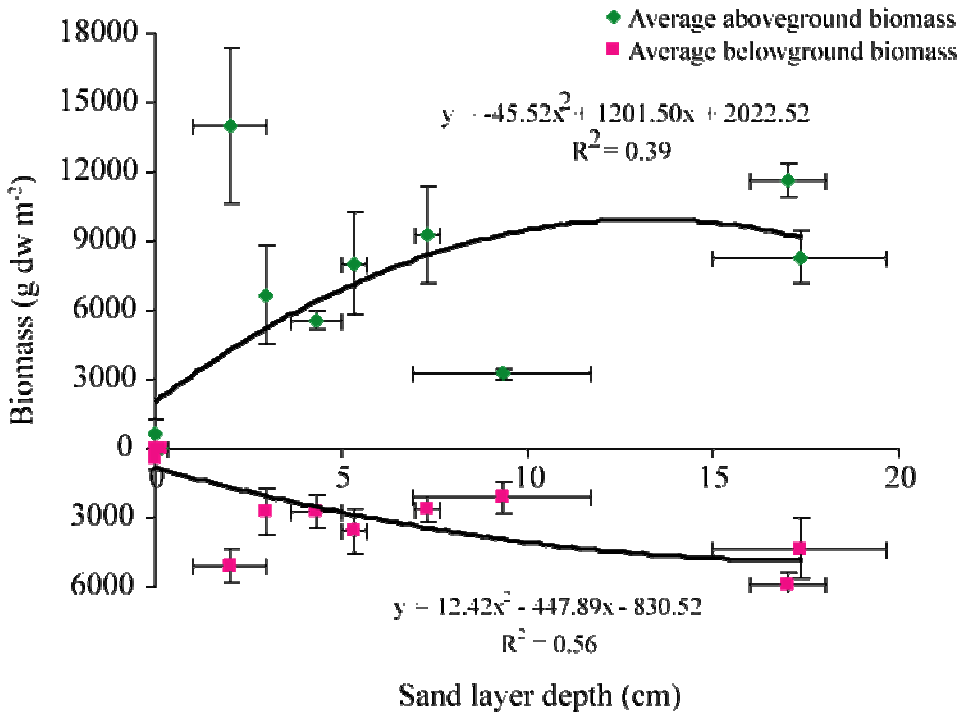

Figure 8: Average aboveground and belowground biomass of *Zostera marina* as a function of sand layer depth at Mill's Island in 2005. Horizontal and vertical lines represent SE.

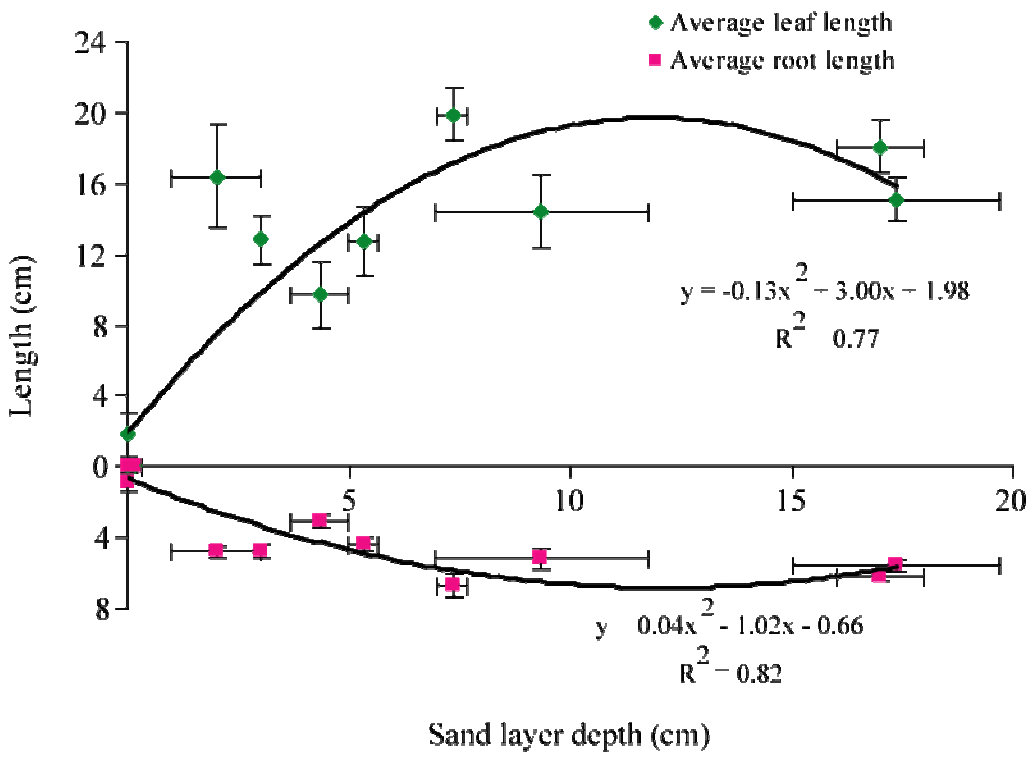

Figure 9: Average leaf and root length of *Zostera marina* as a function of sand layer depth at Mill's Island in 2005. Horizontal and vertical lines represent SE.

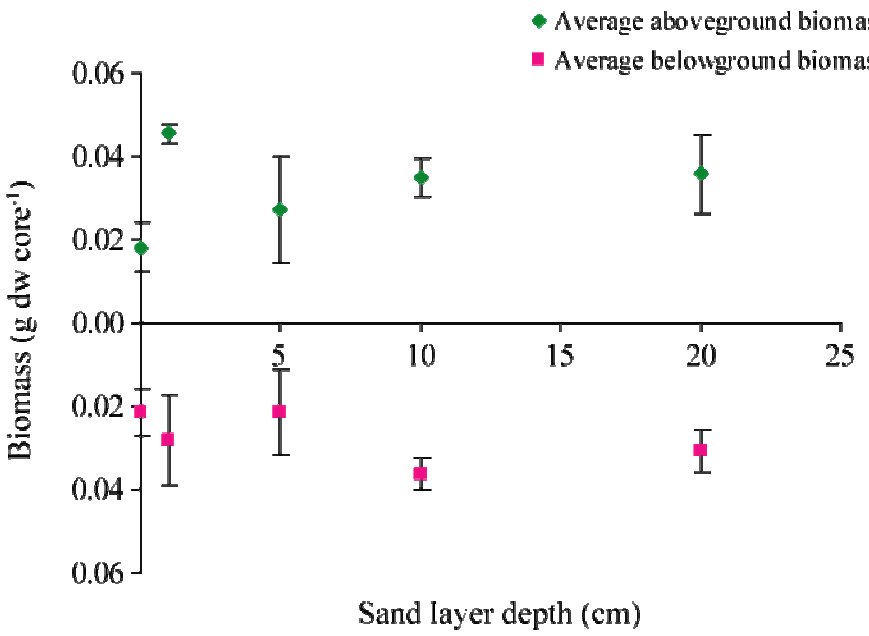

Figure 10: Average aboveground and belowground biomass of *Zostera marina* in sediments with different (0, 1, 5, 10 and 20 cm) sand layer depths in a controlled laboratory experiment. Vertical lines represent SE.

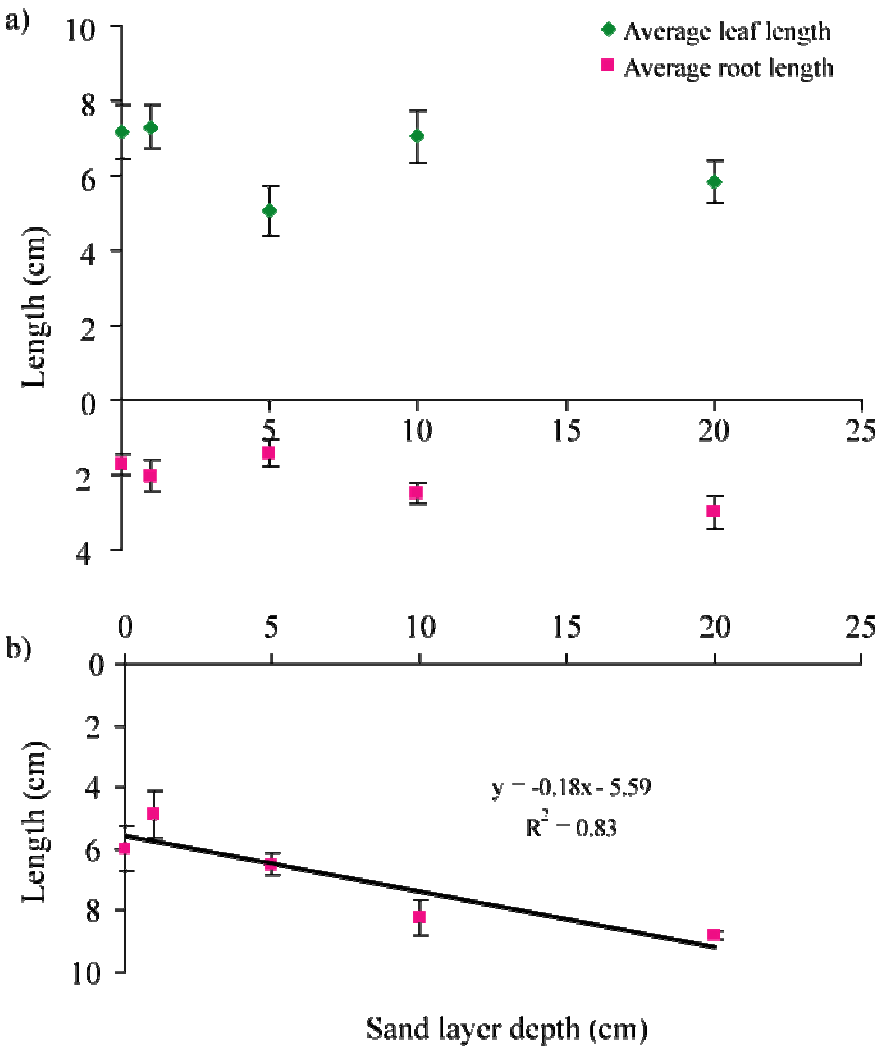

Figure 11: Average leaf and root length (a) and average maximum root length (b) of *Zostera marina* in sediments with different sand layer depths (0, 1, 5, 10 and 20 cm) in a controlled laboratory experiment. Vertical lines represent SE.

were long and thin, which allowed only minimum cleaning of the walls and the plants. Based on observations made throughout the experiment, the plants in 0 and 1 cm sand depth grew best during the first half of the experiment, but then began to slough off leaves during the second half of the experiment, which may be due to epiphytic fouling (Howard and Short 1986, Fong et al. 2000). Additionally, the plants in the 10 and 20 cm sand layer depths did not seem to grow at first, but then began to grow well at the end of the experiment. The plants may have been putting all their energy into belowground growth during the first part of the experiment, and then they began to increase their leaf length and aboveground biomass during the latter half of the experiment. However, there are no measurements to support these suppositions and therefore, the conclusion drawn from this experiment is that sand layer depth influences *Zostera marina* root length, with root length increasing with sand layer depth.

The findings at Mill's Island in 2004 do not follow the same pattern as 2005, possibly due to disturbance by Hurricane Isabel in September 2003. The top layers of sediment, especially the sand, appear to have been eroded away by higher than normal waves and may have led to exposed rhizomes at the northeast edge of the seagrass bed (Figure 12). Additionally, plants that may have been growing in areas with a few cm of sand overlaying old marsh peat may have been washed away with the sand. Therefore, findings from 2004 may represent a special case scenario of extreme events. The findings *in situ* in 2005 support the experimental findings that sand layer depth (if present) is controlling root length, but also show that seagrass aboveground biomass and distribution adjacent to retreating marshes is controlled by sand layer depth. While maximum aboveground and belowground parameters were found when the sand layer

Figure 12: Photograph of exposed rhizomes of *Zostera marina* at Mill's Island in spring 2004 after Hurricane Isabel passed through the area in Septemer 2003. Note that the roots penetrate into the old marsh peat.

depth reached approximately 12 to 13 cm, sand layers as thin as 2 cm also supported a relatively healthy *Zostera marina* bed. These findings confirm those of Zieman (1972) that seagrass growth is determined by the depth of sediment overlaying peat. Due to sea level rise over the past 4000 to 6000 years, mangrove shorelines in Florida have retreated and *Thalassia testudinum* has colonized the subtidal mangrove peat (Zieman 1972). The seagrass beds form in circular deposits of mangrove peat and once established the roots of the plants grow through marine calcareous sediments (5 – 18 cm deep), through mangrove peat and into cracks within the bedrock. The seagrass blade length and density increases with increasing depth of the marine calcareous sediment on top of the peat (Zieman 1972). Based on the results from Mill's Island, a combination of physical and geological parameters may be determining growth and distribution of seagrasses adjacent to retreating marsh shorelines. The sand is fundamental in allowing seagrasses to establish their root system and to anchor themselves in wave-exposed environments. A sand layer approximately as thick as the *Zostera marina* maximum root length (15 cm) seems to lead to the densest seagrass beds, but even thinner sand layers allow for seagrass growth adjacent to retreating marsh shorelines. However, these areas with less sand may be more vulnerable to erosion and loss of seagrasses due to a reduced anchoring capacity. When sand is absent, plants are also likely to be absent due to their morphological unsuitability for these high energy areas (see Chapter 1, Short 1983, Lee and Dunton 2000).

As sea level is expected to continue to rise, it can be assumed that newly available subtidal habitats will continue to present themselves. Adjacent to marshes, these areas will likely be characterized by old marsh peat and may be suitable seagrass restoration

sites because of the relatively easy solution of depositing sand over the old marsh peat. However, it would have to be determined whether currents and waves will transport sand away from the targeted area. Not only might this be a useless endeavor if the sand is transported elsewhere, it may have detrimental effects on other benthic habitats via burial (Mills and Fonseca 2003, Stronkhorst et al. 2003). Therefore, depositing sand over old marsh peat (at least 2 cm) as a possible restoration strategy may be beneficial, but will need to be thoroughly researched before implementing it.

Conclusion

Seagrass distribution adjacent to retreating marshes: a process driven by the organic content of the sediment and sand layer depth.

Sea level rise impacts coastal plant communities, such as marshes, by exacerbating shoreline erosion, increasing the duration and frequency of flooding events and intrusion by saltwater (Ehler et al. 1996, Kearney et al. 2002). The retreat of marsh shoreline via sea level rise leads to new subtidal areas that are potential seagrass habitat. However, the new substrate in these subtidal habitats is old marsh peat, a highly compacted, organic rich sediment. Whether seagrasses can grow in this sediment depends on its sediment organic content and hydrogen sulfide concentrations (Koch 2001, Kemp et al. 2004). Based on *in situ* observations that seagrass habitats adjacent to retreating marshes are usually unvegetated, the hypothesis that old marsh peat adjacent to retreating marshes is unsuitable for seagrass growth due to high organic content and high hydrogen sulfide concentrations was tested.

A series of field surveys and a controlled experiment suggest that hydrogen sulfide in old marsh peat does not appear to affect seagrass growth because the concentrations in the rhizosphere were lower than those found to inhibit photosynthesis (400 μM, Goodman et al. 1995) and growth (1000 μM, Kemp et al. 2004). Additionally, the sediment organic content of old marsh peat (4.4%) is not limiting to seagrasses and indeed, *Zostera marina* grew better in old marsh peat than in lower organic content (< 1%) sediments. Therefore, the original hypothesis was rejected. However, the current study shows that sediment organic content may affect plant morphology (Figure 1). In sediments with high organic content (i.e. high nutrients), such as those found adjacent to

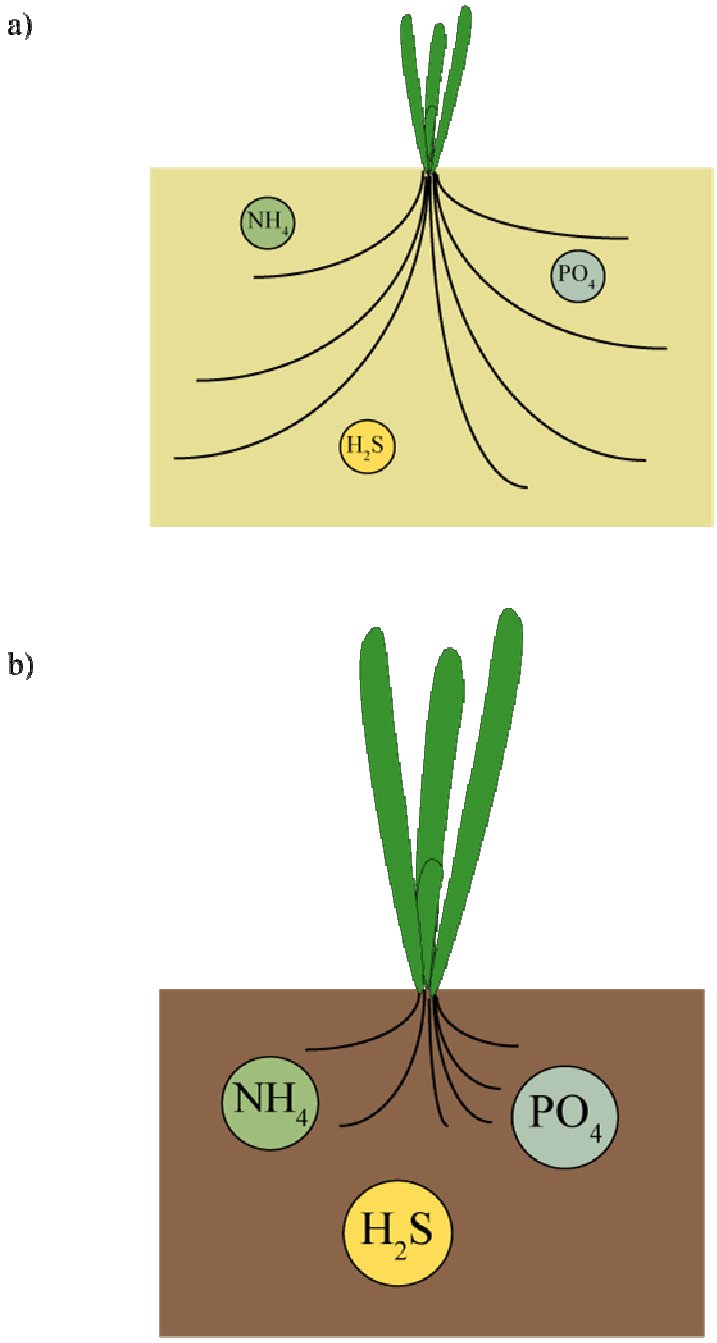

Figure 1: Schematic illustration of the differences in plant morphology of *Zostera marina* growing in organic poor (a) and organic rich sediments (b). Sizes of the nutrient and hydrogen sulfide bubbles represent relative concentrations.

retreating marshes, *Zostera marina* develops short roots and larger aboveground biomass. This morphology is likely to lead to increased drag on the leaves and decreased anchoring capacity by the roots. While this morphology may be suitable for quiescent environments, seagrasses with this type of morphology would likely be pulled out of the sediment by the drag exerted on the leaves in high energy environments (Figure 2). Therefore, the apparent reason for the lack of seagrasses in sediments adjacent to retreating marshes is the combination of high wave energy (as exhibited by the shoreline erosion) and the morphological response of seagrasses to high organic content sediment.

While seagrasses are absent from systems where old marsh peat is the only available substrate adjacent to retreating marshes, they may be present in areas where sand overlays old marsh peat. Seagrasses growing in organic poor sand (i.e. low nutrients) develop small aboveground biomass and long roots that reach far into the sediment (Figure 1). This morphology leads to decreased amount of drag exerted on the leaves and an increased anchoring capacity. In high energy environments, seagrasses with this morphology will likely not get pulled out of the sediment because the increased anchoring capacity. Therefore, the presence of sand appears to be a major factor in determining seagrass distribution adjacent to retreating marshes. Even a thin layer of sand (2 cm) allows seagrasses to grow adjacent to retreating marshes, although there appears to be an optimal sand layer depth of approximately 15 cm (the depth of the rhizosphere) that allows maximum density and biomass.

In conclusion, the combination of sea level rise, local sediment characteristics and local hydrodynamic conditions may result in unvegetated sediments adjacent to retreating marshes, unless there is a natural source of sand which can provide a suitable substrate

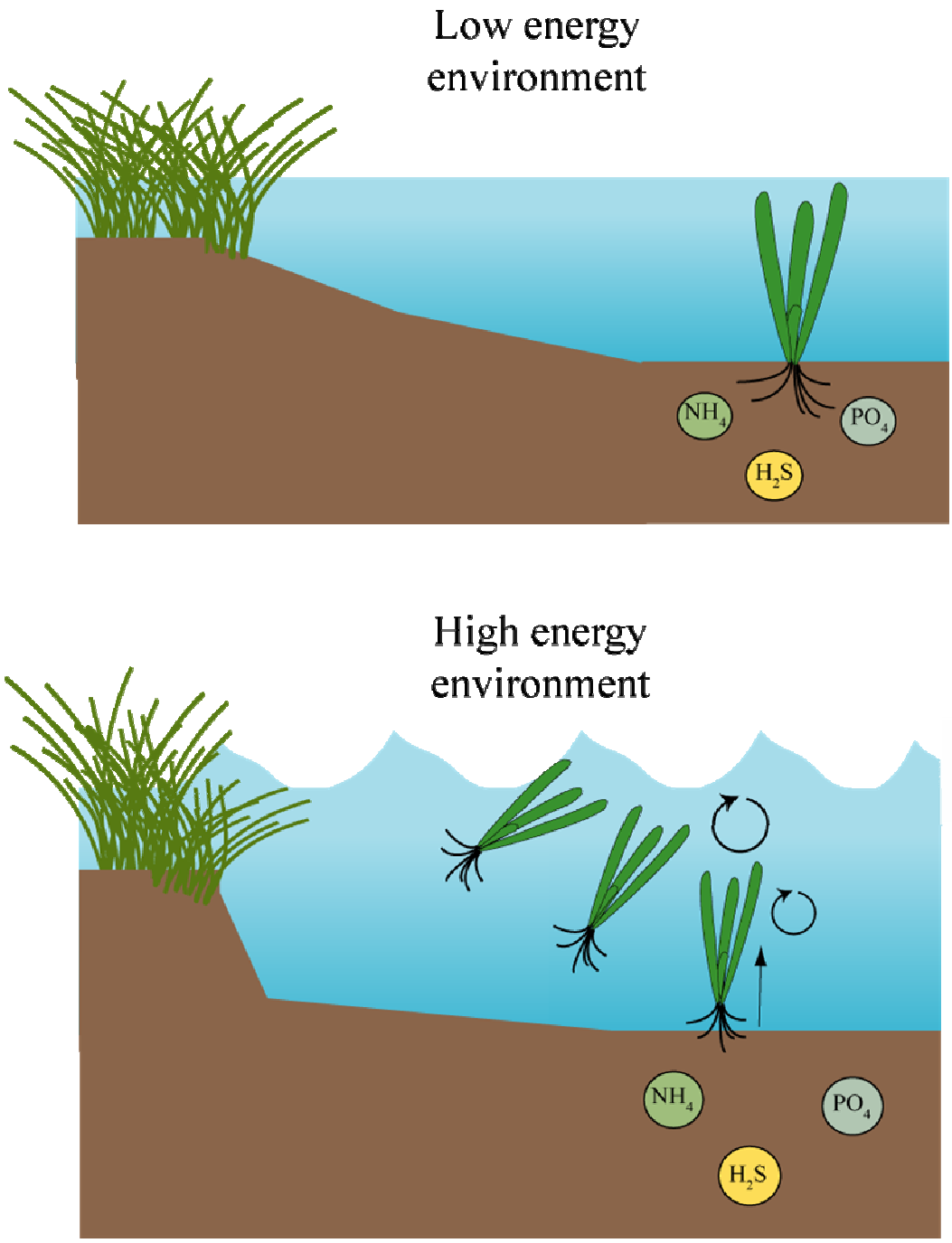

Figure 2: Comparison of plants growing in organic rich sediments under two different hydrodynamic conditions.
Wave action (↻) Seagrasses being uprooted (↑).

for seagrasses (Figure 3). The decision to restore seagrasses adjacent to retreating marsh shorelines will need to be determined by (1) the morphological response of seagrasses to the sediment organic content of the available sediment and (2) by the local hydrodynamic conditions that affect the sediment environment.

Until this study, the effects of sea level rise on seagrasses had not been quantified. Rather, inferences had been made about seagrass growth responses to changing environmental parameters (light availability, tidal range and salinity) associated with sea level rise (Short and Neckles 1999). This research shows that seagrass responses to sea level rise are more complex than previously hypothesized by Short and Neckles (1999) and predicted by Duarte (2002), illustrating the fact that the effect of sea level rise on seagrasses needs to be studied as a whole rather than as individual components. Therefore, an ecosystem approach to sea level rise is needed when addressing the future of seagrasses. Additionally, this study shows that due to sea level rise, the opportunity for seagrasses to move landward may present itself. However, their ability to do so is dependent on a variety of interacting local factors. Therefore, the hypothesis that coastal plant communities will migrate landward as sea level rises (Ehler et al. 1996, Short and Neckles 1999, Duarte 2002) needs to be evaluated on a case by case basis.

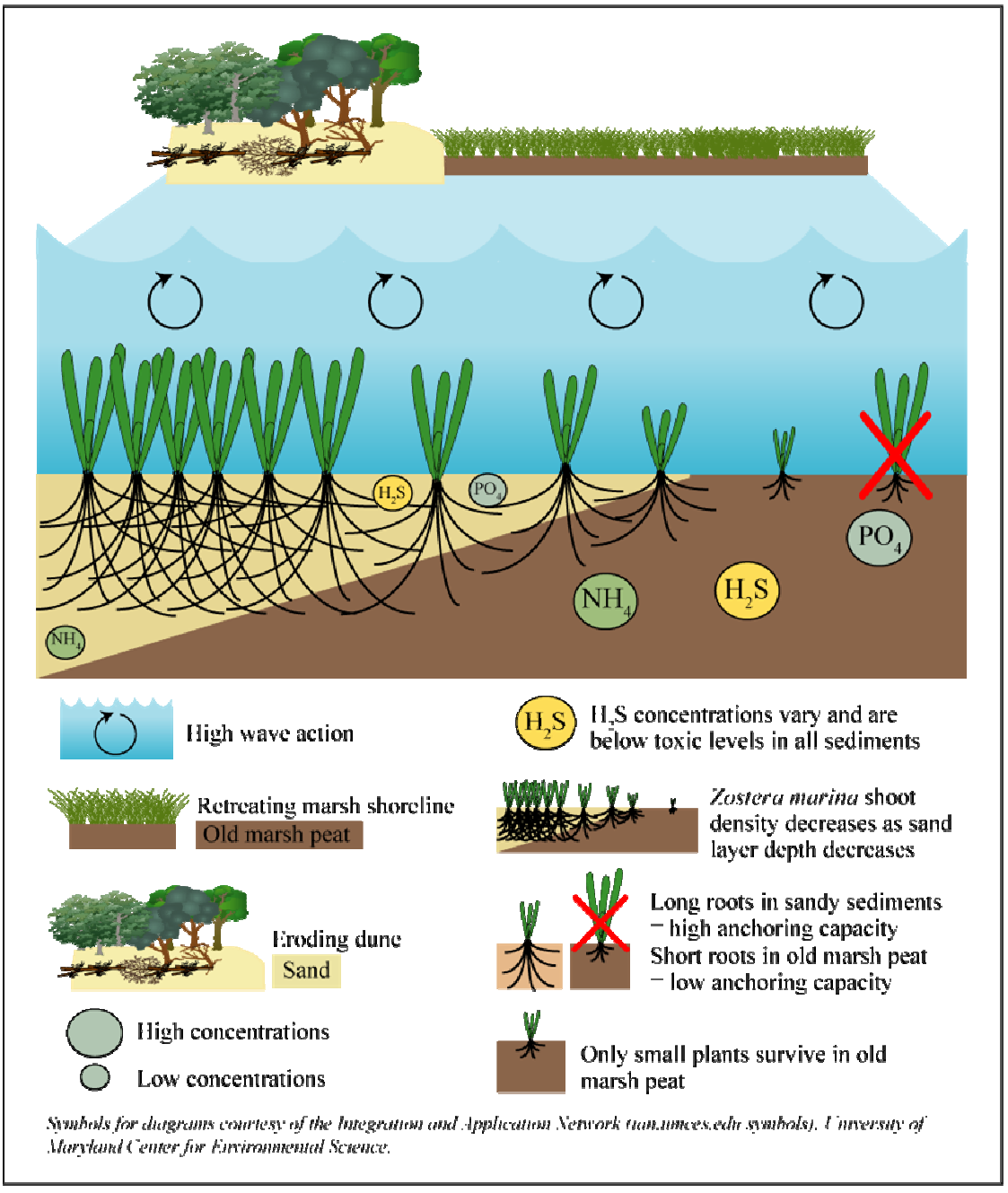

Figure 3: Conceptual diagram of processes leading to seagrass distribution adjacent to retreating marshes.

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